Figure 83. Catches of six most regularly caught species of Suisun Bay in otter trawls of the Bay study through time (northern anchovy excluded).

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The stations of the Fall Midwater trawl survey, upstream of Carquinez Straits, reveal a general decline in the freshwater species of the upper estuary (Figure 84). The decline in striped bass has been widely discussed, but similar declines in other species have received little attention. White catfish (*Ameirus catus*) were one of the most abundant fishes in the first half of the study but they disappeared from the catch following the 1976-1977 drought. The extremely wet year of 1983 was the only time since the earlier drought that white catfish were caught in any abundance. As already described, the other abundant fishes of Suisun Bay and the Delta (American shad, threadfin shad, Delta smelt and longfin smelt) have all declined since the early 1970s. In the three wet years since 1979 the abundances of striped bass and longfin smelt increased to levels that were common in the first eight years of the study. Fish abundances in normal and dry years are lower than any of the catches in earlier years.

Of the eight most commonly captured species in all three months of the fall midwater trawl, all but American shad and northern anchovy are highly correlated with the passage of time. Striped bass, white catfish, threadfin shad, Delta smelt and longfin smelt are all negatively correlated; only yellowfin goby is positively correlated (Table 15).

Table 15. Correlations of each common species of the fall midwater trawl survey with increasing year 1967-1988.

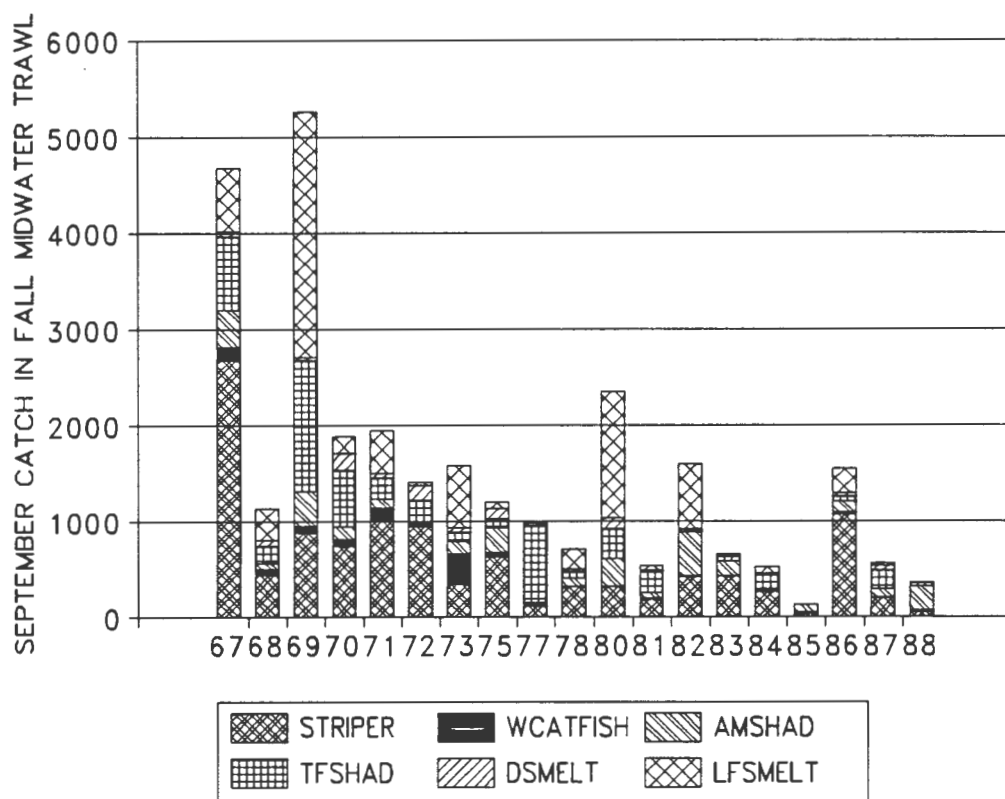| SPECIES	SPEARMAN	PROBABILITY
Striped bass	-.62	< .01
White catfish	-.77	< .01
Threadfin shad	-.66	< .01
Longfin smelt	-.54	< .05
Delta smelt	-.61	< .01
Yellowfin goby	.55	< .05
Northern anchovy	-.10	NS
American shad	-.13	NS

Figure 84. Catch of six most abundant species during September by the fall midwater trawl survey 1967-1988.

The University of California at Davis sampling program is restricted to a small portion of the estuary but is the only sampling program that encompasses shallow slough habitat. Suisun Marsh contains an wide assortment of native and introduced species, formerly in high abundance. Sampling by Sazaki (1975) found native fishes in the Delta to be concentrated in this sort of shallow habitat, but only in waters of the Sacramento River. In 1979 when the University sampling program began, Suisun Marsh was chosen for study because it appeared to support the densest populations of native freshwater fishes in the estuary.

All of the formerly common species of fish in Suisun Marsh have declined over the course of the sampling program (Figures 85 and 86). Even species of broad ecological tolerances, such as carp and Sacramento sucker, are much less abundant than they were in earlier years. Tule perch are the only species that appear to continue to fluctuate in abundance at abundances similar across the 11 years of sampling. Not included in the graphs, because it only arrived in the marsh in 1987, is the introduced chameleon goby (*Tridentiger trigonocephalus*). This species has increased in abundance from less than .25 per trawl in 1987
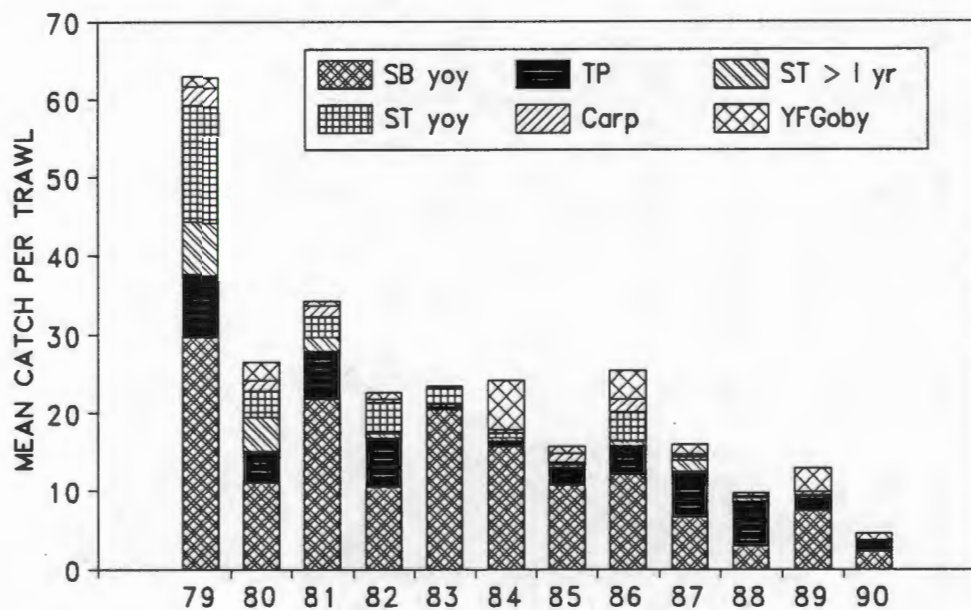
Figure 85 Abundance of six most frequently captured species collected by otter trawl sampling program by UCD in Suisun Marsh.

to more than 4 per trawl in 1990. Because of the decreased catch of all other species the chameleon goby is often among the three most abundant species in monthly catches.
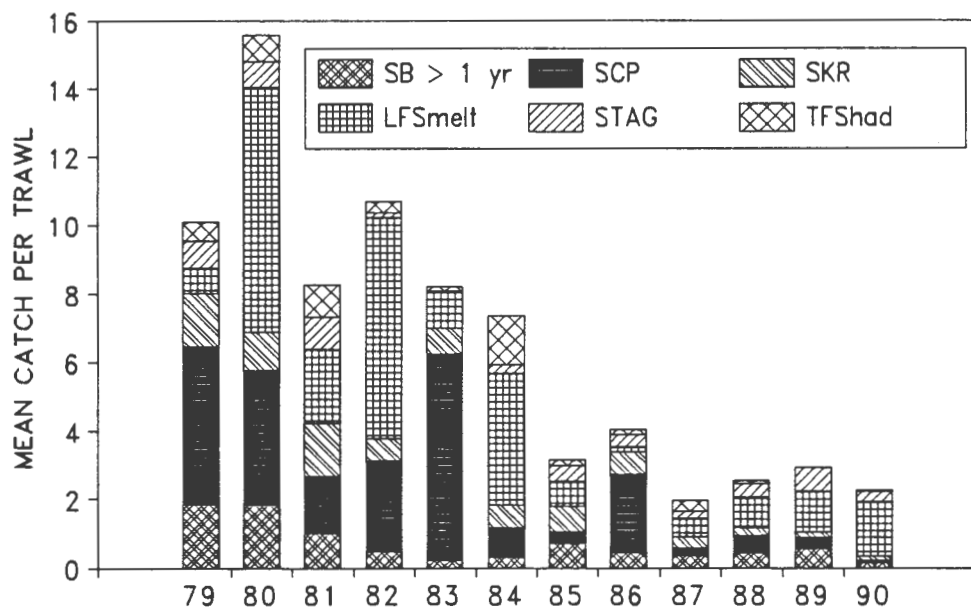
Figure 86 Seventh through twelfth most frequently captured species in sampling of UCD in Suisun Marsh.

6.8.2 Principal Components Analysis

Principal Components Analysis (PCA) is a mathematical technique to reduce the variability within a dataset by identifying combinations of variables that together account for more variability than single variables. The resulting components may be viewed as combinations of variables which vary together, those with negative signs varying inversely but proportionally to those with positive signs. For example, a PCA of wintertime weather variables such as temperature, precipitation, barometric pressure in the Bay Area might yield one component that was positive on temperature and precipitation and negative on barometric pressure, another that was positive on precipitation and negative on temperature and pressure. The analyst might then interpret the first component as indicative of tropical storms, the second as indicative of arctic storms. In this analysis we attempt to use PCA to identify oceanic, estuarine and freshwater groups of species and see which are associated with outflow and diversion rates.

In order to identify the species in each embayment that covaried together across years, we used the yearly total for the selected stations. The lack of correlation in abundance of northern anchovy in South and San Pablo Bays suggested that other species may also use the two embayments differently. We also wished to identify groupings of species characteristic of different outflow regimes. We, therefore, repeated the analysis including the yearly average for total inflow from the rivers and total exports as calculated from the DAYFLOW dataset. Analyses were performed on two measures of species abundance, the total catch for each year and the total number of trawls in which they occurred. These two measures should identify trends within population size and population range. The difference between the two smelts, where one declined in range and the other declined in mean catch led us to seek similar differences in species groups.

Initial analysis of DAYFLOW indicated that almost all interannual variation could be accounted for by total inflow and total exports. The principal components analysis also indicated that these two features were largely independent of each other.

Principal components analysis of the log-transformed data for the eight most abundant species identified two major species associations in each embayment from the Bay Study in both the midwater and otter trawl data (Tables 18-21). White croaker, plainfin midshipman, jacksmelt, topsmelt, English sole, and bay goby were frequently grouped together on one component that also associated negatively with flow. Longfin smelt, Delta smelt, striped bass, staghorn sculpin, and starry flounder were often on components in positive association with total river flows. Northern anchovy, shiner perch, yellowfin goby, and speckled sanddabs were often on components that did not load heavily on outflow or diversion rates. The analyses were repeated using the frequency of occurrence of each species in the trawl so that abundance and distribution could be compared. Differences between the two analyses are small and appear to reinforce each other.

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The linkage of most Suisun Bay species with high outflows and low diversions emphasizes the community-wide level of disturbance that the combined effects of climate and water policies of the period since 1984 has produced.

```
South Bay          Central Bay        San Pablo Bay      Suisun Bay

PC1    PC2         PC1    PC2         PC1    PC2         PC1    PC2
39%    23%         37%    27%         49%    19%         39%    26%

INFLOW             INFLOW             INFLOW             INFLOW
LFSMELT            LFSMELT            LFSMELT            STRIPER
-WCROAK            ENGLISH            STAGHOR            LFSMELT
-MIDSHP            -ANCHOVY           STRIPER            STARRY
-EXPORT            -EXPORT            -EXPORT            -EXPORT
       ANCHOVY            -ANCHOVY    -ENGLISH                  LFSMELT
       BAYGOBY            SHINER             WCROAK             STAGHORN
       ENGLISH           SANDDAB             -ANCHOVY          YFGOBY
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Table 16. Principal components of the Bay Study otter trawl catch based on log10 of total catch in year. Exports and delta inflow are measured as log of million acre-feet.
Only variables with weightings on components greater than .5 are listed.
Percentages give amount of variability in whole data set accounted for by each component.

```
South Bay          Central Bay        San Pablo Bay      Suisun Bay

PC1    PC2         PC1    PC2         PC1    PC2         PC1    PC2
41%    30%         32%    30%         53%    21%         36%    23%

BAYGOBY            INFLOW             INFLOW             INFLOW
ANCHOVY           LFSMELT            LFSMELT            STRIPER
WCROAK            -EXPORT            STAGHOR            LFSMELT
MIDSHP            -ANCHOVY           STRIPER            STAG
-EXPORT                              -EXPORT            -EXPORT
       INFLOW            EXPORT      -ENGLISH                  LFSMELT
       LFSMELT           BAYGOBY            WCROAK            STARRY
       ENGLISH           SHINER             ANCHOVY           -EXPORT
                         SANDDAB
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Table 17. Principal components of the Bay Study otter trawl catch based on frequency of occurrence in year. Exports and delta inflow are measured as log of million acre-feet.Only variables with weightings on components greater than .5 are listed.Percentages give amount of variability in whole data set accounted for by each component.

South Bay		Central Bay		San Pablo Bay		Suisun Bay	
PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
41%	23%	43%	21%	46%	28%	54%	21%
-INFLOW		INFLOW		INFLOW		INFLOW	
TOPSMELT		LFSMELT		LFSMELT		STRIPER	
WCROAK		-WCROAK		-JACKSMLT		LFSMELT	
JACKSMLT		-MIDSHIP		-EXPORT		DSMELT	
MIDSHIP		-EXPORT			ANCHOVY	AMSHAD	
EXPORT			-JACKSMLT		LFSMELT	-EXPORT	
	INFLOW		LFSMELT		-WCROAK		ANCHOVY
	LFSMELT		MIDSHIP				YFGOBY
			WCROAK				

Table 18. Principal components of the Bay Study midwater trawl catch based on log10 of total catch in year. Outflow and inflow rates are given as log10 of measures in million acre-feet. Only variables with weightings on components greater than .5 are listed. Percentages give amount of variability in whole data set accounted for by each component.

South Bay		Central Bay		San Pablo Bay		Suisun Bay	
PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
49%	22%	59%	18%	50%	34%	44%	34%
-INFLOW		EXPORT		INFLOW		INFLOW	
ANCHOVY		MIDSHIP		LFSMELT		STRIPER	
WCROAK		WCROAK		WCROAK		DSMELT	
TOPSMELT		ANCHOVY		MIDSHIP		YFGOBY	
MIDSHIP		LFSMELT		-JACKSMLT		-EXPORT	
EXPORT			LFSMELT		EXPORT	-ANCHOVY	
	INFLOW		INFLOW		ANCHOVY		INFLOW
	LFSMELT				WCROAK		LFSMELT
	JACKSMLT				MIDSHIP		STRIPER
					-INFLOW		ANCHOVY

Table 19. Principal components of the Bay Study otter trawl catch based on frequency of occurrence in year. Exports and inflow are given as log of million acre-feet. Only variables with weightings on components greater than .5 are listed. Percentages give amount of variability in whole data set accounted for by each component.

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7 INFORMATION NEEDS

7.1 General overview

An important need for restoring the healthy fisheries which the Estuary has supported in the past is to develop an understanding of the estuary as an ecosystem. Attention to date has largely focussed on particular species or particular areas with little effort to coordinate studies. Development of a general, descriptive model of the aquatic habitats and resources of the Bay and Delta is necessary. To date, species have received attention largely in a crisis management attitude: collapse of fisheries in the Bay was dealt with by removing most commercial fisheries, loss of spawning habitat for salmon was addressed by building hatcheries, massive entrainment of young fish by diversions is avoided by trucking hatchery salmon further downstream and by supporting commercial hatcheries for striped bass. The declines of numerous species which depend on the Delta and Suisun Bay habitats should provide convincing evidence that there is a general environmental problem rather than a series of species-specific problems. Solving the problem from a unified and scientific approach is likely to be more effective and efficient than a piecemeal approach.

In order to attain a useful understanding of the estuarine ecosystem several steps are needed:

1. Determine patterns of use for the major species of each embayment, regardless of their *prima facie* economic value. For example, northern anchovies are the most abundant fish in the Bay but it is unclear to what extent they actually spawn in the Bay, how much of their feeding represents a loss of food for other fishes, or how much of the anchovy population that enters the Bay represents productivity from the ocean that becomes food for animals in the Bay.

2. Determine the productivity of the various parts of the estuary and identify where the food for aquatic animals comes from. The movement of food materials between areas is an essential part of the determination of productivity possible by animals in each area. Appendix A represents a first effort toward this problem and illustrates the value of a community approach. Suisun Bay has been described as an important nursery area because of the presumed high productivity there. If this is the case and the nursery value of Suisun Bay rests on food inputs from river flow, then no manipulation of salinity or flow pattern within Suisun Bay can compensate for reduced river outflow.

3. Determine the trophic connections of the aquatic resources of the Bay. Knowing the amount of food that is available generally is insufficient to estimate the production of higher trophic levels unless the energetics of the trophic system are known. Food habits of the animals of the Sacramento-San Joaquin estuary are poorly known so that the abundance and distribution of lower trophic levels provides little information on the production of higher levels. Production of *Melosira*, *Sinocalanus*, or *Potamocorbula* is unlikely to provide the same fish abundances as equivalent densities of *Asterionella*, or *Eurytemora*. Simply determining the number of trophic levels would provide a much more sound basis for estimating potential fish production.

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4. Identify the sources of mortality, and mortality rates for representative species in each habitat. Focussing research on a long-lived species like striped bass has permitted shorter-lived species to approach extinction. Sensitive species could provide an effective early warning system for disruptions to the environment of the Bay and Delta, rather than simply being the species most apt to become extinct.

To develop this sort of ecological understanding of the estuary requires more work than can reasonably be expected by agencies before more species go extinct under the present budgetary restrictions.

Recent coordination of effort of university researchers with agency researchers has yielded answers to significant questions regarding the feeding success, dietary habits and physiological stresses in striped bass and new information on the breeding biology of the threatened Delta smelt. The increased involvement of the academic community has been due partly to an active program by state agencies to encourage them. The Interagency Ecological Studies Program and the San Francisco Estuary Project initiated the University Academic Research Involvement Program which should help increase university interest in the Estuary. Atlantic estuaries have a long and fruitful history of cooperation among agency and university personnel.

7.2 Ecological data and information gaps relative to productivity

Phytoplankton productivity. Changes in the array of sampling stations are warranted. Two issues in particular need to be addressed. First, primary productivity in shoal areas dominates that in deeper areas, especially in Suisun Bay, yet most data are collected from channel stations. Second, almost no long-term series of chlorophyll or productivity measurements are available for Central and San Pablo bays. Little is known, consequently, about the entrapment zone when it is pushed out of Suisun Bay by high flows. Third, certain areas in South and Suisun bays appear to be oversampled in space, relatively speaking. In the South Bay, for example, the region between San Bruno Shoal and the Dumbarton Bridge exhibits much less spatial variability than the region between the Golden Gate Bridge and San Bruno Shoal. A similar analysis of data landward of the Carquinez Strait reveals tight clusters of stations, such as from Chipps Island to Point Sacramento.

Time series for the Bay are thus characterized by periods with relatively high frequency data, and regions with relatively high-resolution data, interspersed with long gaps in time and space. The irregularity in sampling hinders the potential value of the data that are collected, particularly for understanding the long-term changes that may now be underway globally. A commitment needs to be made to a group of "index stations" that will be sampled at a regular frequency for at least chlorophyll *a* and extinction coefficient (or, equivalently, photic depth) into the indefinite future. Some of the current effort in the channels should be shifted to shoal sites. Similarly, some of the current efforts in South and Suisun bays should be shifted to Central and San Pablo bays. If this basic, "index station" program is made as simple as possible, its longevity would be more likely. The number of stations and the sampling frequency should

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therefore be as modest as possible. The abundance and distribution of benthic organisms should be carefully considered in choosing index stations, as the benthos provide a kind of "integrated moving-average" indication of chemical and planktonic conditions.

Actual primary productivity measurements are not necessary, as productivity can be deduced from biomass, turbidity, and light availability (Sec. 6.2.1). But given the importance of light availability, a permanent station should be established for measuring surface irradiance. The absence of continuous, reliable, irradiance measurements hinders the interpretation of existing data sets.

Assumptions about aphotic respiration have a large effect on estimated productivity, particularly in Suisun Bay. Yet little direct evidence exists on the magnitude of these respiratory losses. Further experimental work on aphotic respiration in San Francisco Bay would be a definite contribution, particularly work that would improve estimates of net water column productivity P_{nw}.

Benthic microalgal productivity. No measurements have yet been made on benthic microalgal productivity, despite their possible significance, especially in South and Central bays. As discussed previously, prevailing measurement techniques may be unreliable. Although suitable methods may not be available for San Francisco Bay, this issue does require more attention. At the very least, sampling of sediment chlorophyll could accompany water column measurements at index stations. The product of sediment chlorophyll and light incident on the sediments could serve as a relative index of benthic productivity. Incident light could be estimated from measurements of surface irradiance and extinction coefficient (photic depth) at the sampling stations.

Delta discharge. Delta discharge may be the largest source of organic matter for Suisun Bay and is probably a significant one for the northern reach as a whole. The load of organic carbon to San Francisco Bay from the Delta needs to be measured on a regular basis. Due attention needs to be given to POC as well as DOC, and to bottom samples as well as near-surface samples. Because of the probable episodic nature of organic carbon loading, sampling must be able to resolve the succession of storms that characterize the winter period. Because of the apparent importance of riverine algae, chlorophyll and derived pigments also should be measured in tandem with organic carbon.

The issue of availability needs to be addressed as well. BOD measurement offers one perspective on this problem. Ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.) need to be continued and extended. Additional approaches also must be sought.

Tidal marsh export. Tidal marsh sources may be of importance for Suisun Bay, particularly during drought periods. Direct estimates of tidal marsh export are virtually impossible, in part because of the difficulty in determining residual flows from tidal exchange. The uncertain availability of exported organic carbon is another obstacle. Hence, indirect methods are required

to address this question. The use of multiple stable isotope markers appears to be of value. B.J. Peterson et al. (1985), for example, using ^{13}C, ^{15}N, and ^{34}S, was able to show that benthic macroinvertebrates consumed *Spartina* detritus and plankton in preference to terrestrial plant detritus. A similar study in Suisun Bay may be able to determine at least the qualitative significance of tidal marsh export.

In view of the large export of reduced sulfur encountered for some marshes (Peterson et al. 1980), a preliminary investigation of sulfide oxidation activity related to tidal marsh exports is warranted.

Circulation and mixing. The system boundaries need to be considered carefully in relation to physical transport. At the minimum, transport through the Golden Gate requires definition and should be the first objective. A carbon budget for the entire Bay would then be feasible.

Further subdivision needs to be done carefully, with due regard to topographical features and the existing data. As implied in the previous discussion, the segmentation scheme normally used landward of the Golden Gate requires some revision. The boundary between South and Central bays, in particular, perhaps should be shifted to the San Bruno Shoal. The northern extent of "Central Bay", currently at Point San Pedro-Point San Pablo, also requires re-examination from a hydrodynamic point of view. In addition, the utility of the boundary between San Pablo and Suisun bays needs to be addressed. The entrapment zone, as well as organic matter from riverine loading, moves freely across the boundary as flows increase. From the point of view of establishing subregions for a carbon budget and subsequent food web analysis, the distinction between the two subembayments may have little value. On the other hand, a further subdivision of South Bay at the Dumbarton Bridge appears warranted, in view of the higher point source loading, relative tidal marsh area, and runoff south of the bridge. A lack of primary productivity measurements in lower South Bay would be an impediment to this subdivision, something to be considered also in the choice of index stations (see above).

Whatever the boundaries, direct measurements of transport are an unrealistic goal, for the same reason that tidal marsh export cannot be assessed with any accuracy. But the flow field can be characterized from existing data and modeling studies. In principle, the flow data can be combined with concentration data for various organic matter fractions to estimate transport across the major boundaries. In practice, the concentration data does not appear to be adequate in many locations. Modelling studies, therefore, must be accompanied by a supplemental field measurement program for organic matter fractions, particularly DOC, various size fractions of POC, and chlorophyll. At the minimum, measurements are needed at the Golden Gate, including horizontal gradients through the Gate and vertical profiles both seaward and landward of the Gate.

Food web structure. The structure of the food web connecting organic carbon sources to higher organisms is critical in determining the magnitude of their food supply. The number of trophic linkages, for example, is especially important in controlling the efficiency of energy transfer from sources to macroscopic consumers: If energy is transferred with an average efficiency of,

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say, 10% along each link, then the interposition of an intermediary organism has the same effect as a ten-fold drop in the food supply at the base of the food web.

At the macroscopic level, food webs have been delineated in a number of ecosystems, as recently reviewed by Schoener (1989). At the microscopic level, on the other hand, the relative importance of many postulated pathways has not yet been demonstrated (Mann 1988), for the Bay or for other ecosystems. In view of the nature and number of these microscopic interactions -- involving autotrophs, DOC, bacteria, protozoans and small metazoans -- a complete characterization of the Bay's food web appears to be an unrealistic goal for the near future.

It is possible, nevertheless, that a complete characterization is unnecessary. Circumstantial evidence from other ecosystems suggests that the major pathways through the food web are sometimes relatively simple. Demersal fish production, for example, often has a high efficiency when compared to organic carbon sources for the benthos (reviewed by Mann 1982). Energetic considerations require that settling organic matter be consumed directly by macrofauna and passed to demersal fish in order to account for this high efficiency. If the other components of the benthos do, indeed, have a secondary role, then the current lack of quantitative knowledge regarding bacteria, microfauna, and meiofauna in San Francisco Bay sediments (Nichols and Pamatmat 1988) may not be a major impediment. Note, however, that the "small food web" consisting of micro- and meiofauna does compete for food with the macrobenthos of some estuaries (e.g., Wadden Sea; Kuipers et al. 1981).

A comparison of benthic macroinvertebrate productivity (e.g., Nichols 1977) with primary productivity would be especially pertinent, particularly during bloom periods when most of the annual phytoplankton production takes place. If macroinvertebrate productivity were a high enough percentage of microalgal productivity, then a direct link from primary producers to the large benthic invertebrates would be implicated. Lower percentages would imply either that intermediate consumers were present in the water column or sediments, or that the planktonic food web was a significant sink for organic matter. A related study in the South Bay is currently in the initial planning stages (J. Thompson 1990, pers. comm.). A similar investigation is warranted for Suisun Bay. The results of these studies, combined with ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.), should provide a guide for further research within the benthic habitat.

Even though the major pathway *within* the benthic habitat may be simple, organic matter from primary productivity may undergo transformations *before* coming into contact with the benthos. For instance, the close relationship in San Francisco Bay between bacterial activity and biomass, on the one hand, and phytoplankton productivity, on the other (T. Hollibaugh 1990, pers. comm.) points to a "microbial loop" (Azam et al. 1983) in this estuary. Bacterial processes also may play an essential intermediary role between allochthonous sources of organic matter and larger planktonic or benthic invertebrates. Riverine phytoplankton, for example, must undergo osmotic stress within the vicinity of the entrapment zone, probably liberating organic material for bacterial processing. Also, detrital material from upstream may be colonized by

bacteria and rendered more desirable and nutritious for consumers such as *Neomysis mercedis*, which often has abundant detritus in the gut (Kost and Knight 1975). The number of trophic links in the water column may radically affect the food supply to midwater fish and the benthic habitat, whether these links occur on a microscopic or macroscopic level. A continued investigation into planktonic microbial processes is therefore warranted. The detailed study of mechanism, however, should be accompanied by attempts to determine whether a simple pathway dominates. As in the case of the benthos, simultaneous measurement of both organic matter sources and production of the larger planktonic invertebrates may provide the necessary clarification. These measurements would be most informative if done in conjunction with those for the benthos.

The pathway of energy through the estuary's food web is largely conjectural, except for a few well-studied species and small areas. Meioplankton (rotifers, protozoa, etc.) have been almost completely unexamined, but as an additional trophic level, they could represent a major reduction in the amount of fixed carbon that is available to higher trophic levels.

Trophic studies of aquatic resources in San Francisco Bay and Delta have focussed almost entirely on striped bass, which show strong seasonal and age shifts in food habits. There is no reason not to expect similar complexity in the dietary habits of many other species. Without such knowledge the effects of changes in productivity on higher trophic levels is very loose conjecture.

The emphasis of research on an introduced, rather weedy, fish species has delayed recognition of the status of several native species. Secondarily, the emphasis on striped bass has limited the scope of subsidiary studies to a restricted geographic part of the estuary. Studies based on more sensitive species, on species representing a diversity of habitats within the estuary and on species of diverse trophic patterns would allow a much more accurate and sensitive monitoring of conditions. Thus, perhaps we could develop an ecological understanding that would allow us to progress past the pattern of emphasizing a single species that has characterized the management of sardines, salmon and striped bass.

7.3 Sampling procedures and programs

Zooplankton studies of the estuary have been largely concerned with documenting the food chain affecting striped bass. Consequently, zooplankton data for Central and South Bay are extremely sparse. Because food webs in these embayments probably rest on autochthonous production, an understanding of the role in consumption played by the abundant seasonal species (particularly northern anchovy) is crucial to determining the amount of energy available as food for resident species.

The absence prior to 1980 of any regular, year-round sampling of fishes in most of the estuary has severely restricted the possible analyses of status and trends. Without a regular sampling program for the benthos, zooplankton, and fishes throughout the estuary, the effects of water policy changes, climatic shifts, and species introductions will remain a confused mix

of suspected causes and observed effects. Underfunding of this project in 1989 and 1990 led to cessation of sampling for some months at a time when several species were showing the effects of extended periods of low river outflow. Similar interruptions in other sampling program during an earlier drought probably deprived us of information that may have been important in understanding the effects of drought on fishes. The commitment of adequate funds to these programs, and the personnel necessary to run them, is of the greatest importance in protecting and understanding the resources of the Bay.

In 1966 (Turner and Kelley 1966; Kelley 1966) a description of the fishes and invertebrates of the Estuary covered the distribution, abundances and life history of most of the dominant species. The importance of dead-end sloughs, both in terms of their high concentrations of food and as principal habitat for many species was suggested by preliminary surveys. The importance of these habitats to several species was further emphasized in surveys conducted by Sazaki (1975). Since then several excellent reviews of biological work done in the Estuary have appeared (e.g. Conomos 1979, Cloern and Nichols 1985, and Nichols et al. 1986, as well as many reports to the State Water Resources Control Board). However, in looking at how to protect Delta smelt from extinction it has become clear that we have too little knowledge to be able to identify spawning areas or habitat requirements for any of the fishes that use shallow channels in the Delta. Identification of the critical habitat of this species will have to encompass a larger region than is perhaps necessary in order to be sure of adequate protection. A number of other species may also be headed for the listing process (such as longfin smelt and Sacramento splittail) which also probably rely on shallow Delta habitats for spawning. Sampling programs are needed to determine specific habitat requirements of native fishes and the extent to which the species of the Delta can be managed as a community.

Tributary streams to the Bay are isolated fragments of habitats which support or have supported 10 of the 17 fish species endemic to the Central Valley as well as populations of several listed species, including the freshwater shrimp (*Syncaris pacifica*). These streams also support remnant populations of steelhead, chinook salmon and coho salmon. These streams, then, are significant reservoirs of California's biodiversity but they have been the subject of little research but major habitat alteration (Leidy 1984). Surveys are needed to identify which streams are still home to these heritage resources, how they might be preserved, and their importance as organic carbon contributors or as spawning habitat for species of the Bay.

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Status and Trends Report on
AQUATIC RESOURCES

TECHNICAL APPENDIX

ORGANIC CARBON SOURCES FOR THE FOOD WEB OF
SAN FRANCISCO BAY

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SUMMARY

1. The sources of food and energy for estuarine food webs are diverse. These sources include primary production within the estuary (autochthonous sources); organic materials flowing into the estuary from the rivers, land, and atmosphere (allochthonous sources); and exchange with the ocean (transport sources; Fig. A.1). The first step in assessing food availability to higher organisms in the Bay is a systematic accounting of these sources. They are usually measured in the common currency of "organic carbon" content.

2. The Bay was divided into South, Central, San Pablo, and Suisun bays for assessing organic carbon sources. Hypsographs and related morphometric data were assembled for each subembayment (Table A.2, Fig. A.2).

3. Estimates were made of each organic carbon source for each subembayment using a variety of techniques. Phytoplankton productivity was estimated from a morphometric model and measurements made in 1980 (Table A.3, Fig. A.3). Benthic microalgal productivity, seagrass productivity, and tidal marsh export were estimated from habitat area in conjunction with the range of values (on the basis of unit area) published for other estuaries. Delta discharge, point sources, nonpoint source runoff, atmospheric deposition, spills, and dredging sources were all estimated from data collected for San Francisco Bay. Macroalgal productivity, photosynthetic bacterial productivity, groundwater contributions, and biotic transport could not be estimated quantitatively, but were assessed on the basis of qualitative considerations. Transport due to circulation and mixing could not be estimated.

4. The available data permitted a comparison of the different carbon sources for 1980. Phytoplankton productivity, benthic microalgal productivity, and Delta discharge of organic matter probably were major sources ($>25\%$) for at least one subembayment. Tidal marsh export, point sources, and dredging transport probably were significant secondary sources ($>10\%$) for at least one subembayment, but never major sources. Seagrasses, macroalgae, photosynthetic bacteria, runoff, atmospheric deposition, spills, groundwater, and biotic transport appear to have been minor sources ($<10\%$ total), regardless of subembayment.

5. For San Francisco Bay as a whole, phytoplankton productivity was the dominant and only major source (50%), and benthic microalgal productivity was the only significant secondary source (20%). All other sources contributed less than 10% of the total. Comparisons for the whole Bay, as well as for each subembayment, assume that only about one-tenth of Delta discharge was actually available to the food web.

6. For South Bay, phytoplankton productivity was the dominant source (60%) in 1980, but benthic primary productivity was probably a major source (30%) as well.

Since 1980, annual phytoplankton productivity in the photic zone of the channel has fluctuated within a factor of two, but no long-term trend can be observed. Productivity tends to increase with annual Delta discharge, apparently because higher Delta outflow promotes stratification of South Bay waters. Stratification, in turn, leads to higher growth rates and lower losses to suspension-feeding benthic macroinvertebrates. Productivity thus may remain low as long as Delta outflow is depressed. The lack of long-term data for shoal phytoplankton (accounting for 60% of total phytoplankton productivity) and benthic microalgae prevents more certain conclusions.

7.   Phytoplankton productivity (40%) and benthic microalgal productivity (30%) appear to have been the major sources of organic carbon for Central Bay in 1980. Point source loading (10%) and transport of dredging spoils from adjacent subembayments (10%) could have been significant secondary sources.

Insufficient data exist to characterize interannual variability of phytoplankton or benthic microalgae since 1980. The available evidence suggests that mechanisms for phytoplankton variability in Central Bay are different from those in South and San Pablo Bay, including possibly a major influence from the coastal ocean. Point source loading continued to decline after 1980. Dredging exhibits much interannual variability, but with no trend.

The usual boundary separating South Bay from the central basin for analytical purposes needs to be reconsidered.

8.   San Pablo Bay was dominated by phytoplankton productivity (60%) in 1980. Benthic microalgal productivity (20%) and marsh export (20%) may have been significant secondary sources of organic carbon.

No long-term data exist for shoal phytoplankton, which accounted for almost 80% of the estimated phytoplankton productivity. However, the mechanisms controlling interannual variability in San Pablo Bay are thought to be similar to those in Suisun Bay.

9.   The dominant organic carbon source for Suisun Bay probably was riverine loading from the Delta (60%) in 1980, even when only one-tenth is considered available as food. Marsh export (20%) and phytoplankton productivity (10%) may have had a secondary role. Much of the organic matter contributed in Delta discharge seems to have been phytoplankton and its breakdown products.

The current drought period that began in 1987 is a time of depressed Delta outflow and, presumably, depressed riverine loading of organic matter. Phytoplankton productivity also has been low since 1983. The low phytoplankton productivity has been attributed to two mechanisms. First, the entrapment zone, which retards advective losses of phytoplankton from its vicinity, is absent during periods of extremely high or low Delta outflow. Second, suspension-feeding estuarine invertebrates become established during periods of prolonged

drought and are responsible for increased grazing losses. Tidal marsh export could actually be a major organic carbon source at present.

The invasion of the corbulid clam *Potamocorbula amurensis* in 1987 may lead to the persistence of high grazing losses even after the drought ends, due the clam's tolerance for freshwater conditions. If so, autochthonous productivity could remain low and riverine loading (and tidal marsh export) would be even more important as an organic carbon source.

10. Evidence from hydraulic residence times, benthic invertebrate consumption rates, and oxygen consumption suggests that most organic carbon sources in the South Bay enter the food web. The same can be said for the northern reach as a whole. On the other hand, organic carbon sources for Suisun Bay -- particularly riverine loading -- may actually be consumed downstream in San Pablo or upper Central Bay.

11. Based on empirical generalizations from a synthesis of work at other estuaries, as well as the apparent importance of food supply for zooplankton in Suisun Bay, a decline of total fish production in San Francisco Bay -- particularly the northern reach -- could have accompanied the decline of organic carbon sources since the early 1980s. The applicability of these empirical generalizations, however, is uncertain for San Francisco Bay. Further, conclusions can only be made about the relation between organic carbon sources and *total* fish production, not the production of any one population, on the basis of these generalizations.

During drought conditions, relatively more of the organic carbon supply may be shunted through benthic, rather than planktonic, pathways, favoring a relative increase in demersal fish.

12. Suggestions were made for future monitoring and research programs regarding phytoplankton and benthic microalgal productivity; Delta outflow of organic materials; tidal marsh export; circulation and mixing; and food web structure.

A.1 INTRODUCTION

A.1.1 Significance of organic carbon budgets

The sources of food and energy for organisms at the base of estuarine food webs are diverse compared to those of other ecosystems. This diversity arises from several features characteristic of estuaries. Tidal fluctuations create intertidal habitat for benthic micro- and macroalgae, and marsh for higher plants. Rivers carry in food materials from upstream, as well as inorganic nutrients to support photosynthesis by phytoplankton and other primary producers within the estuary. Finally, sewage and other waste products of nearby human communities are often a source of food for microbial populations and, ultimately, for the food web supporting higher organisms.

Because characteristics such as morphometry, river discharge, and human population densities differ so much from one estuary to another, the exact mix of potential food sources is unique to each estuarine system. Because of this diversity and uniqueness, it is not possible to understand the existence of or potential for food limitation of higher organisms -- the larger invertebrates, fish, sea mammals, and birds -- without first undertaking an explicit accounting of the types and amounts of food entering at the base of the food web.

If the various food sources are to be compared, they must be expressed in terms of a common currency. Organic carbon units rather than energy units are used here, as the former is more often measured on field samples. In practice, one usually describes food sources in units of either organic carbon or energy simply because the information rarely exists to undertake a more sophisticated characterization. The ramifications of this simplification must be kept in mind, however. Food acts as a source of structural material and energy, but it also provides specialized molecules (e.g., vitamins); the actual food value of a substance cannot be fully characterized in a single dimension. The mere fact that a substance contains reduced carbon does not mean that it can be ingested or assimilated by organisms. By virtue of size, shape or chemical composition, food materials may be partially or entirely unavailable to consumers. For most food sources, however, there is little information on availability to primary consumers and the organic carbon or energy values must be accepted at face value. This issue is particularly relevant to the interpretation of river-borne organic carbon and we return to it later in connection with Delta discharge.

The "accounting" of various food web pools and fluxes in terms of organic carbon is usually referred to as a "carbon budget." Carbon budgets can assume various levels of detail. The most basic budget, which we shall examine here, consists of all sources and sinks for the organic carbon pool as a whole -- in other words, a one-compartment model -- considered on an annual basis. The internal dynamics of the organic carbon pool are not treated at all at this stage, nor are the total organic carbon (TOC) fluxes fractionated into such categories as dissolved organic carbon (DOC) and particulate organic carbon (POC). These further refinements, if found to be desirable -- and possible -- can be constructed on the basic carbon

budget as a foundation. The effort necessary to provide other than a basic budget does not conform at all to the time constraints of the current report. In addition, an adequate treatment of the Delta could not be accomplished for this report, which is therefore confined to San Francisco Bay. It was believed preferable to accomplish at least part of the task as well as the data permitted, rather than to provide more superficial but broader spatial coverage. The current treatment, despite its brevity and inadequacies, at least can serve to motivate and orient an ongoing analysis aimed at greater accuracy, more spatial coverage, and finer resolution in both space and time.

The basic budget does include all sources of organic carbon arising within the estuary ("autochthonous" sources), as well as organic carbon which is transported into the estuary ("allochthonous" sources). These sources must balance sinks of organic carbon within the estuary plus transport of organic carbon from the estuary. As our goal here is to clarify the nature of energy flow *into* the food web, sinks or losses from the organic carbon pool will not be treated explicitly. When sink terms can be completely characterized, they are of value in solving mass balance equations for the magnitude of certain sources that cannot otherwise be quantified. In the case of the San Francisco estuary, however, the uncertainty in source and sink magnitudes precludes such an approach.

Not all processes can be characterized a priori as either a source or a sink. For example, tidal exchange can potentially act as either, depending on the gradient of carbon across the mouth of the estuary and other factors. It seems most useful, at the beginning, to classify processes according to whether they are definitely a source, definitely a sink, or have the capacity to be either a source or sink, depending on the circumstances. The first two kinds can be thought of as "unidirectional" processes, the last kind as "bidirectional" or perhaps "exchange" processes of unknown net sign. Note that exchange processes may be biotically mediated -- for example, fish migration into or out of the estuary -- as well as due to physical processes.

Many processes of potential importance can be specified (Fig. A.1). Some of these turn out to be clearly of importance in the San Francisco estuarine system, others clearly negligible. Still others -- perhaps the majority -- cannot yet be established with any useful accuracy. Despite the large amount of good research that has been accomplished in the estuary, development of a carbon budget has never been an explicit goal. As a result, we understand certain processes in detail (e.g., phytoplankton production) and others not at all (e.g., benthic microalgal production). The present undertaking cannot remedy this problem. But by making these gaps in our understanding explicit, the current endeavor can summarize existing knowledge systematically and contribute to a rational approach for orienting further research. In particular, we seek to answer a certain sequence of questions: What organic carbon sources can be identified as clearly important components of the total flux into the organic carbon pool? What sources might be important? What sources are probably negligible? In this manner, the basic carbon budget and its refinements can serve as a useful conceptual framework for understanding the dynamics of the San Francisco estuary, as it has for many other estuaries.

ORGANIC CARBON POOL

- Unidirectional sources
  - Autochthonous
    - phytoplankton
    - benthic microalgae
    - seagrasses & epiphytes
    - macroalgae & epiphytes
    - photosynthetic bacteria
  - Allochthonous
    - Delta discharge
    - tidal marsh export
    - point sources
    - runoff
    - atmospheric deposition
    - spills
    - groundwater

- Exchange processes
  - circulation and mixing
  - dredging activity
  - biotic transport

INTERNAL ORGANIC
CARBON FLUXES

Unidirectional sinks

Figure A.1 Sources for the San Francisco Bay organic carbon pool.

The annual carbon budget itself is a function of time, not a collection of static quantities. Many of the fluxes contributing to the budget must change from one year to the next, and their relative importance thus may change as well. Unfortunately, estimates for each flux are available only for one or a few years, often not overlapping. In view of the lack of data, it seems pointless to attempt an explicit budget for each individual year. Nevertheless, as many fluxes that appear to dominate the carbon budget were in fact measured during 1980, a year of "intermediate" Delta outflow, we eventually use 1980 as a reference point and attempt a budget for that year. Using this budget and various other considerations, we try to delineate those processes that were probably negligible both in 1980 and subsequent years, even in the face of strong year-to-year variability. For the remaining processes, the following questions are also addressed: What interannual changes can be identified, and what were the underlying reasons? What do these causal mechanisms imply about these fluxes since 1980 and in the coming years?

In addition to "best estimates" for each carbon source, an attempt will be made to arrive at an *uncertainty range*. It will be assumed in some cases that the possible values can be approximately described by a normal distribution; the estimate will be set equal to the mean and the uncertainty range will be set equal to the 95% CL. A true normal distribution is actually impossible in many of these cases, such as when a flux is physically constrained to be nonnegative. For other carbon sources, both the estimate and the uncertainty range will be based on the range of literature values, but with no assumption of an underlying distribution. The estimate need not necessarily be at the midpoint of the range. The choice of estimates and

uncertainty ranges obviously has a subjective component that could lead to error. For many poorly-studied processes, for example, future measurements may be found to lie outside the range. Erring in the other direction, certain values reported in the literature may represent extreme situations that result in an unnecessarily large uncertainty range for San Francisco Bay. Despite the approximate nature of these ranges, they serve to caution the reader regarding the validity of "best estimates" of carbon flux. Furthermore, despite the large sizes of many of the uncertainty ranges, deductions are still possible concerning the relative importance of different carbon sources.

All estimates are rounded off to at most 2 digits. The second digit is retained to prevent roundoff errors in the first digit, but probabaly only one digit is significant. When a value is reported in the form $x \pm s$, x refers to the mean but s may refer to the standard deviation (SD), standard error (SE), or 95% confidence limits (95% CL); the exact meaning will be stated.

A.1.2 Morphometric considerations

In constructing a carbon budget, it is first necessary to specify what is considered to be within the estuarine boundaries. Here, we include both the open water of the four major subembayments -- South Bay (SB), Central Bay (CB), San Pablo Bay (SP) and Suisun Bay (SU) -- as well as all other wetlands in tidal contact with this open water. Together, these subembayments will be said to constitute San Francisco Bay (SF). The aquatic boundaries between these subembayments are as specified in the Aquatic Habitat Institute Bay-Delta segmentation scheme (Gunther 1987). The shore boundaries are somewhat harder to delineate, due to seasonal and interannual variation in habitat characteristics. Aside from open water, the shore boundaries considered here encompass intertidal mudflats, vegetated tidal marsh, tidal channels, and rocky shore (see ABAG 1989 for a detailed treatment of wetland habitat classification). An independent assessment was not made for the region south of the Dumbarton Bridge, as certain critical data were not available separately for this area; the relative importance of carbon sources, however, could very well be different from the rest of South Bay.

Morphometric data come from several sources. Data for all open water habitat deeper than mean lower low water (MLLW) were provided by the United States Geological Survey (USGS; J. Burau 1990, pers. comm.). These data, for the nodes of a 0.25-km grid covering the entire Bay, were interpolated from nautical charts (Burau and Cheng 1989). A hypsometric curve referenced to the MLLW tidal datum was constructed for each major embayment using these data and the AHI segment boundaries (Fig. A.2, which shows the results only down to 20 m). These curves illustrate, in effect, "typical" cross-sections through the respective embayments. Central Bay clearly stands apart from the others due to its relatively steep slopes. The remaining embayments have quite similar hypsographs, although San Pablo Bay has the highest proportion of shoal area, as evidenced also by its median depth (Table A.1).

Morphometric data for areas above MLLW were taken from other sources. In particular, the areas at mean tidal level (MTL) and mean higher high water (MHHW) were required for our

Table A.1

Morphometry of San Francisco Bay and its four major subembayments
referenced to the MLLW tidal datum.

Bay	Area $(10^8 \ m^2)$	Volume $(10^9 \ m^3)$	Depth Mean (m)	Depth Median (m)	Depth Maximum (m)
SB	4.7	1.9	4.0	2.2	29
CB	2.2	2.5	11	7.7	99
SP	2.6	0.86	3.3	1.5	29
SU	1.0	0.31	3.1	1.8	28
SF	11	5.5	5.3	2.3	99

Note: Based on the the segmentation scheme of Gunther (1987)
and the methods of Burau and Cheng (1989).

analysis. First, published values of MTL and MHHW, referenced to the MLLW datum, were
averaged for each subembayment (USCOE 1977). Next, the values for MLLW, and thus MTL
and MHHW, were referenced to the National Geodetic Vertical Datum (NGVD), again averaged
for each subembayment (USCOE 1984). The areas between MLLW and both MTL and MHHW
were then determined from tidal stage-area graphs referenced to the NGVD (Morrison 1988).
Finally, these incremental areas were added to the data for MLLW as previously determined

Table A.2

Water surface area of San Francisco Bay and its major
subembayments at various tidal stages.

Bay	MLLW $(10^8 \ m^2)$	MTL $(10^8 \ m^2)$	MHHW $(10^8 \ m^2)$
SB	4.7	5.5	6.1
CB	2.2	2.4	2.5
SP	2.6	3.2	4.4
SU	1.0	1.2	1.7
SF	11	12	15

Note: Data for MLLW are from Table A.1. The remaining
estimates are based on a variety of sources, as described
in the text.
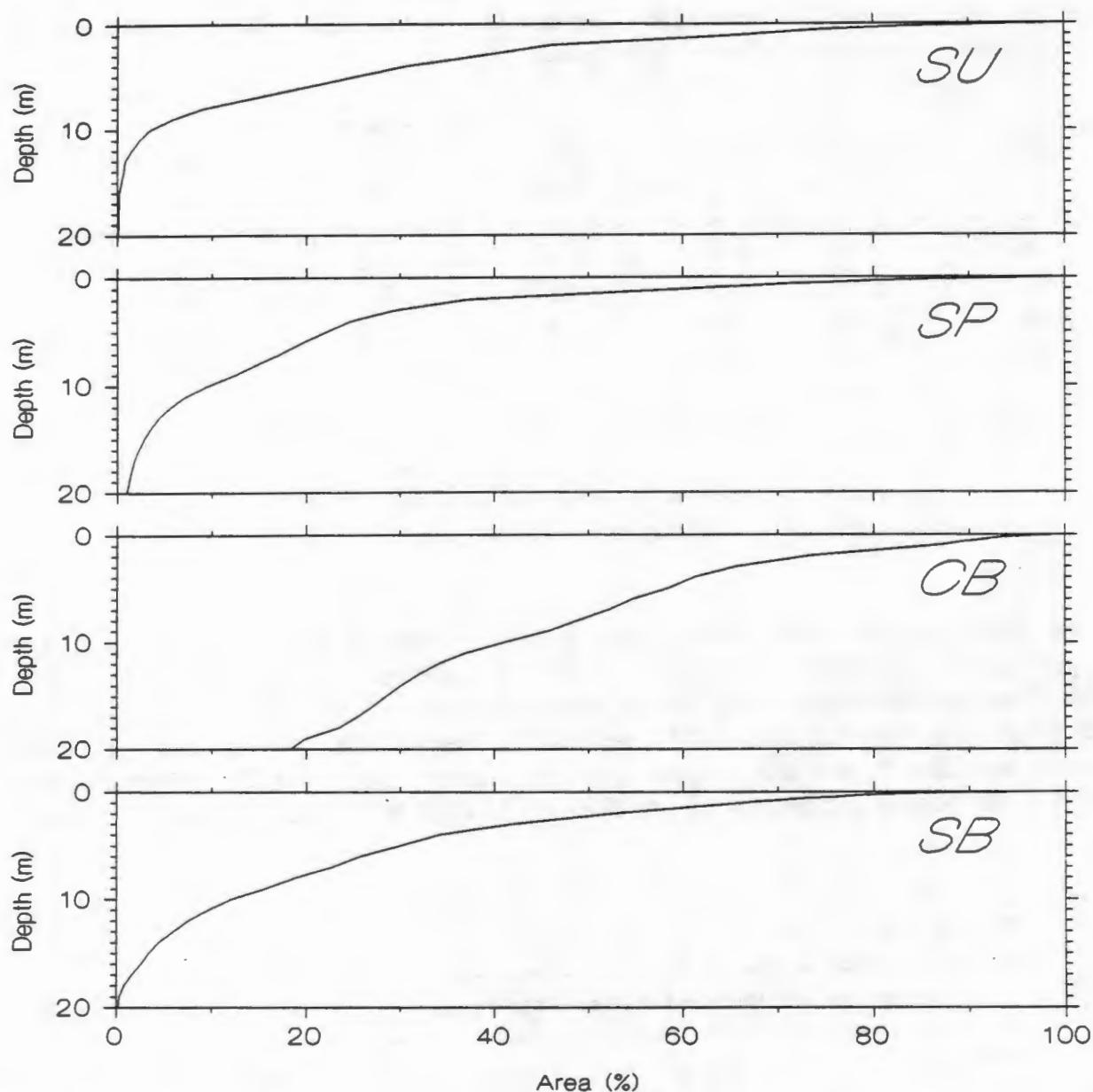
Figure A.2 Hypsographs for the major subembayments of San Francisco Bay (based on the segmentation scheme of Gunther [1987] and the methods of Burau and Cheng [1989]).

from the USGS data (Table A.2; see below for additional information regarding Suisun Bay MHHW).

Areas for specific habitat types were also required for estimates of certain carbon fluxes. Habitat areas for USGS quadrangle maps were determined from the National Wetlands Inventory (NWI) habitat maps for 1985 and then partitioned among various subembayments (M. Josselyn

1990, pers. comm.). The partitioning did not correspond exactly with the AHI segmentation scheme; in particular, Central Bay habitat was allocated to either South Bay or San Pablo Bay.

For Suisun Bay, the area corresponding to MHHW was particularly difficult to determine because of the flatness of the hypsograph in the vicinity of MHHW. As this portion of the hypsograph was actually determined with the aid of NWI maps (Morrison 1988), it was decided to use the NWI data for mudflat and tidal marsh directly to define the area between MLLW and MHHW (Table A.2). As far as the carbon flux estimates are concerned, this discrepancy is an issue only for estimates of benthic microalgal production. Furthermore, although habitats do not have to correspond to any particular tidal datum -- tidal marsh could occur both below MLLW and above MHHW, for example -- the assumption does not affect our conclusions in any way.

A.2 AUTOCHTHONOUS CARBON SOURCES

A.2.1 Phytoplankton

Of the autochthonous organic carbon fluxes to the Bay's food web, phytoplankton productivity has been studied in the most detail (Cloern et al. 1985 summarize and interpret the numerous phytoplankton studies). A particularly valuable data set for the purpose of estimating annual production was collected in 1980, when productivity was determined monthly at six representative stations, including a shoal and channel site in each of South Bay, San Pablo Bay and Suisun Bay (Cloern et al. 1985). Estimates were based on ^{14}C uptake rates in 24-hr incubations under simulated in situ conditions. Respiration rates in the dark were assumed to equal 10% of the maximum (light-saturated) ^{14}C uptake determined from these 24-hr incubations.

The results for these six stations can be converted to estuary-wide estimates of phytoplankton productivity. Because of the estuary's turbidity, positive net primary productivity is confined to a thin layer near the surface where incident light energy is sufficient, the *photic* or *euphotic* zone. The ^{14}C measurements yield an estimate of net productivity within this layer, a quantity known as the *net photic zone productivity* P_{np} (g C m^{-2} d^{-1}). P_{np} usually overestimates the organic carbon assimilation in the entire water column because of phytoplankton respiratory losses below the photic zone. A more relevant quantity is the *net water column productivity* P_{nw}, which is simply P_{np} corrected for estimated respiration below the photic zone. The size of the correction depends on the depth of water, so P_{nw} is actually a function of depth even in regions where P_{np} is constant.

The depth Z_p of the photic zone -- usually taken to be the depth by which surface insolation is reduced to 1% -- is a few meters, at most, and varies continuously in both space and time with the changing turbidity. The area over which phytoplankton production takes place also changes significantly with the tide (Table A.2). Because of this complex and dynamic situation, several simplifications and assumptions were necessary to convert the monthly measurements to estuary-wide production estimates (Fig. A.3). First, the water level was assumed to be constant at MTL. Next, each subembayment was divided into a "shallow" and "deep" region at 2 m below MLLW (approximately 3 m below MTL), within each of which net photic zone productivity P_{np} (g C m^{-2} yr^{-1}), biomass concentrations b (mg Chl *a* m^{-3}), respiration rates below the photic zone r (g C m^{-3} yr^{-1}), and Z_p (m) were assumed to be constant and equal to the annual means determined in 1980. Then, P_{np} was integrated separately over the shallow and deep region, resulting in estimates of net annual photic zone productivity π_{np} (g C yr^{-1}) for each region. Some adjustments were necessary for the margins of each subembayment where photic depth Z_p is greater than the water column depth Z_m. In particular, it can be shown theoretically under certain simplifying assumptions that shoal regions falling entirely within the photic zone have a P_{np} equal to 0.785 of the P_{np} in deeper water where $Z_p < Z_m$. Finally, using the hypsometric data, the volume below the photic zone was determined for both shallow and deep regions. The hypsometric curves were assumed to be linear between
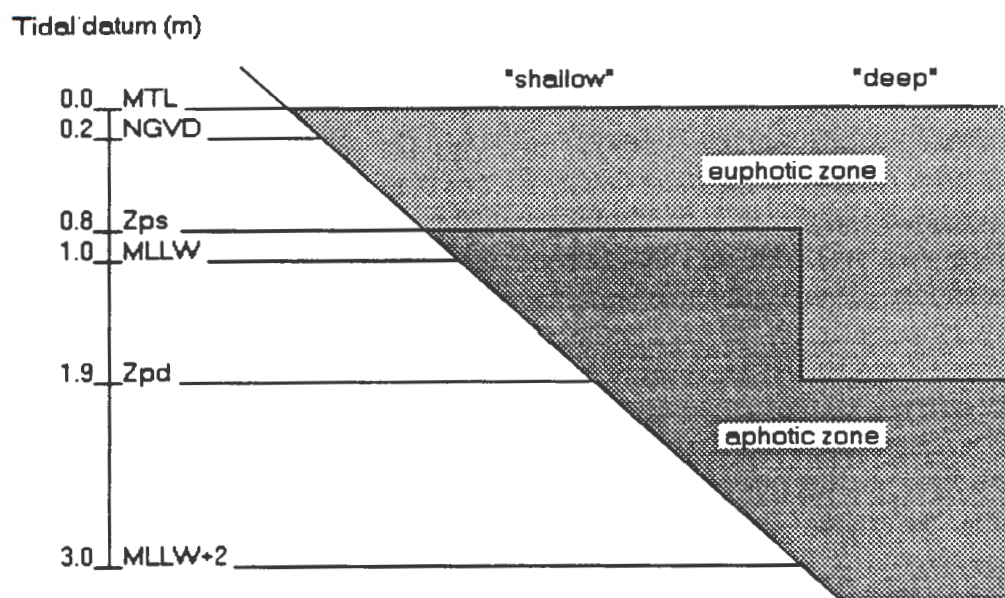
Figure A.3 Schematic cross-section of subembayment illustrating morphometric model used in the estimation of phytoplankton productivity. Values given are for San Pablo Bay.

MLLW and MTL. Respiratory losses were estimated for shallow and deep regions separately and subtracted from the corresponding values for π_{np}, resulting in estimates for net annual water column productivity π_{nw} (g C yr^{-1}).

Central Bay measurements were not reported as part of the intensive 1980 study. Annual values for net photic zone productivity, biomass and photic zone depth are estimated to be P_{np} = 140 g C m^{-2} yr^{-1}, b = 2.5 mg Chl a m^{-3}, and Z_p = 3.1 m, respectively (Cloern 1987, Fig. 7), without using separate values for shallow and deep regions. A biomass-standardized respiration rate r^b (g C [mg Chl a]$^{-1}$ yr^{-1}) of 3 was typical of the 1980 data for the other subembayments (except for an anomalous value for South Bay shoals; Cloern et al. 1985) and was used to arrive at an estimate of r = 7.5 g C m^{-3} yr^{-1}.

Because respiration rates for the aphotic zone of aquatic habitats are so controversial, the data are presented with and without respiration corrections (Table A.3). The data clearly demonstrate how aphotic respiration assumptions have a marked effect on production estimates, accounting for a 30% decrement in net photic zone production for the estuary as a whole and over 50% in the case of Central and Suisun Bays. The differences among subembayments in the importance of aphotic respiration reflects morphometry rather than phytoplankton activity. The

assumption used in Table A.3 -- that r is 10% of light-saturated P_{np} -- may be an overestimate, perhaps even a large one (e.g., Smetacek and Passow 1990).

Respiration, however, is by no means the only source of uncertainty in these estimates. The ^{14}C method itself is characterized by a certain imprecision in the measurement of uptake rates, usually about 10%. Moreover, a number of systematic biases in estimating ^{14}C uptake may be present, including effects due to confinement within bottles, toxic trace metals, "dark bottle" correction, incubation time, and sample fixation (Leftley et al. 1983). An additional underestimate may occur if extracellular products of photosynthesis -- which can sometimes exceed 50% of carbon uptake (Joint and Morris 1982) -- are assimilated and respired by bacteria during the incubation. Further uncertainties are introduced by ignoring the effects of vertical circulation, the existence of vertical and especially horizontal heterogeneity, as well as the presence of tidal marsh vascular plants below MTL that may compete with phytoplankton for insolation. The latter may be a problem especially in Suisun Bay, where California bulrush (*Scirpus californicus*) extends below MTL increasingly from the Carquinez Straits to the Delta (Josselyn 1983). It is not possible to characterize all, or even most, of these uncertainties quantitatively; we can assume, however, that the uncertainty range suggested by respiration alone (Table A.3) should be expanded significantly.

Table A.3
Net annual phytoplankton carbon production for San Francisco Bay and each of its major subembayments.

Bay	π_{nw} (10^9 g yr^{-1})	π_{np} (10^9 g yr^{-1})	$(\pi_{np}-\pi_{nw}):\pi_{np}$ (%)	Shoal π_{nw} (%)
SB	71	86	18	61
CB	15	30	51	55
SP	39	56	31	76
SU	4.7	11	57	110
SF	130	180	29	66

Note: Net annual water column productivity π_{nw} is calculated by assuming that phytoplankton respiration below the photic zone equals 10% of light-saturated ^{14}C uptake; net photic zone productivity π_{np} assumes that phytoplankton respiration is negligible below the photic zone. Shoal π_{nw} is the percent of π_{nw} occurring in water shallower than 2 m referenced to MLLW. All values are rounded to two digits, but probably only one is significant.

A recent study by Alpine and Cloern (1988) offers some additional information regarding uncertainty. These investigators compared growth rates based on both cell division and ^{14}C uptake at four different sites throughout the Bay, including a simulation of two different mixing conditions for each site. The ratio of the two measures among samples was 1.0 ± 0.8 (95% CL) (Alpine and Cloern 1988, Table 2), implying that there was no systematic error in deducing productivity from ^{14}C uptake but the uncertainty was high for individual samples. An uncertainty range of *at least* $\pm50\%$ appears to be warranted.

A.2.2 Tidal marsh vascular plants

Estimates have been made of annual primary productivity for marsh vascular plants at selected sites throughout the Bay (summarized by Josselyn 1983). The values almost all fall within the range of 500 to 1500 g dry wt. m^{-2} yr^{-1}. No clear difference emerges in the productivity ranges for the dominant salt marsh plants Pacific cordgrass (*Spartina foliosa*) and perennial pickleweed (*Salicornia virginica*); the few higher values were associated with bulrush (*Scirpus californicus* and *S. robustus*) in brackish marsh. Most of the studies estimated annual production either on the basis of a single above-ground end-of-season harvest of live tissue (i.e., maximum live dry weight) or by attempting to account for changes in live and dead tissue over shorter intervals (i.e., the Smalley method).

Both of these methods are known to underestimate production by ignoring losses through decomposition, tidal export and import, leaching from leaves, and herbivory (Hopkinson et al. 1980; Long and Mason 1983). The largest errors are due to ignoring decomposition losses and tidal exchange, with tidal exports usually exceeding imports. Leaching losses are minor compared to shoot production, and grazing losses usually smaller still. The underestimate of production is a serious one, typically by a factor of two or three and sometimes higher. Although the Smalley method is usually more accurate than the maximum live dry weight method, curiously enough a single end-of-season measure of maximum standing crop -- both living and dead dry weight -- often gives the best estimate.

An additional underestimate arises from ignoring below-ground primary productivity (Good et al. 1982). Based on data for smooth cordgrass (*Spartina alterniflora*) on the Atlantic coast, the ratio of below-ground to above-ground annual production appears to average between two and three (Schubauer and Hopkinson 1984). No such comparisons are available for San Francisco estuary tidal marsh plants, but the root-shoot biomass ratio for Pacific cordgrass was estimated to average 3.6 (Mahall and Park 1976), which is typical of smooth cordgrass (Good et al. 1982). There is little reason to believe the ratios of below- to above-ground production will not be comparable as well.

Both Atwater et al. (1979) and Josselyn (1983) estimate that emergent vascular plant productivity averages 800 g dry wt. m^{-2} yr^{-1} in the San Francisco estuary, reflecting studies that use maximum live dry weight of above-ground biomass or the Smalley method. As little can be said about differences between subembayments at this point, the 15 Bay studies tabulated by

Josselyn (1983, Table 27) must be treated on an equivalent basis; converting to carbon using a C:dry wt. ratio of 0.4 (Westlake 1963) yields an average of 420 ± 70 (SE) g C m^{-2} yr^{-1} above-ground productivity for these studies. Based on the previous methodological comments, the actual mean may be quite higher. The discrepancy among the methods is so variable, however, that applying a simple "correction factor" must be considered to be unreliable. As a result, an estimate of above-ground tidal marsh contributions was made by taking these field measurements at face value.

Tidal marsh habitat areas for each subembayment were derived from NWI habitat maps (M. Josselyn, 1990 pers. comm.). Although the habitat area for Central Bay was partitioned between South Bay and San Pablo Bay, the Wetland Habitat Map for San Francisco Bay (E. Chan Meiorin 1990, pers. comm.) suggests that Central Bay tidal marsh habitat is negligible. The partitioning of Central Bay thus has little effect on the values given for South and San Pablo bays. Applying the above-ground productivity estimate to the respective habitat areas resulted in the following tidal marsh vascular plant productivity values for each of the four subembayments (10^9 g yr^{-1}):

SB	15
CB	0
SP	28
SU	18
SF	59

Note that the studies tabulated by Josselyn (1983) were conducted during the period 1968-1982 and that the NWI habitat area data were determined for 1985. Assuming that no trend existed in primary productivity on an areal basis, these subembayment estimates thus should be identified with 1985 conditions. As implied in the previous discussion, the stated averages have an uncertainty of $\pm33\%$ (95% CL) due to differences among sites alone. An additional, perhaps large, systematic underestimate may be symptomatic of the methods used.

Below-ground productivity probably contributes an even greater amount of annual production. In view of the lack of any measurements in the estuary and the large range of values reported in the literature, it is perhaps best to refrain from a quantitative estimate of below-ground production. Because of its confined location, the significance of below-ground production to estuarine energy flow outside of marsh sediment may be smaller than for above-ground production (Schubauer and Hopkinson 1984). But it should be noted that export of below-ground organic carbon can be a significant contributor to the total export, especially in sandy soils. For example, Yelverton and Hackney (1986) estimate an export of 52 g C m^{-2} yr^{-1} due to pore water flux alone from a North Carolina *Spartina* marsh.

The above annual mass contributions of carbon must therefore be considered an underestimate, perhaps even by an order of magnitude. In a later section, tidal marsh is considered from an alternative viewpoint, namely, as an allochthonous source of exported organic carbon for other habitats in the estuary.

A.2.3 Benthic microalgae

The distinction between those algae that prefer the pelagic ("phytoplankton") and those that prefer the benthic habitat ("benthic microalgae") is often unclear, both because of settling of algal cells from the water column and resuspension of cells from the sediments (Nichols and Pamatmat 1988). A separation on the basis of preferred habitat, however, need not be of concern here. We need only distinguish between production in the water column and production on the sediments, regardless of what algal types are actually involved in each habitat.

The benthic microalgal community in the estuary has been examined in several studies (reviewed by Nichols and Thompson 1985a), most notably in terms of chlorophyll by Thompson et al. (1981) and in terms of species composition by Laws (1983, 1988). J.H. Gregg and A.J. Horne (pers. comm. 1991) are in the process of analyzing one of the more extensive spatial and temporal surveys of benthic chlorophyll to date (16 stations measured quarterly during water year 1989, and one of these stations sampled 10 times over 18 months). As no measurements of benthic microalgal productivity appear to have been published, however, the only recourse is to estimates based on habitat area and measurements reported in the scientific literature for other systems. Only the crudest of estimates is possible at this stage, both because of the large range of areal production values attributed to other estuaries and the difficulty in defining the relevant habitat areas.

The actual measurement of benthic primary productivity entails unusual technical difficulties, whether measurements are determined through O_2 production, ^{14}C uptake or O_2 gradients. None of the existing measurements in estuaries can be said to be without serious controversy (Admiraal 1984). Furthermore, productivity responds to substrate and a host of environmental factors; although the same can be said for most other natural plant stands, the dynamic nature of the environment is particularly marked in the intertidal zone. Thus, even if the methods were unassailable, the spatial and temporal heterogeneity would still require unusually extensive sampling to adequately characterize annual production (Shaffer and Onuf 1985). The cumulative errors inherent in published estimates imply a great deal of uncertainty.

Several researchers have tabulated results from benthic primary production studies. Knox (1986a) and Colijn and de Jonge (1984), for example, summarize data from over 30 separate sites, including tidal flats and vegetated tidal marsh. As pointed out by the latter authors, most of the annual production values fall within 50 to 200 g C m^{-2} yr^{-1}, even though the sites are at widely different latitudes. Most of the exceptions could be explained by extreme conditions (e.g., polar estuaries). Other recent studies not tabulated by these authors also fall within the stated range (e.g., Shaffer and Onuf 1985; Varela and Penas 1985; Fielding et al. 1988). We thus adopt this range as the uncertainty range, and the midpoint -- 120 g C m^{-2} yr^{-1} -- as the best estimate, for average benthic primary production for the various subembayments of the San Francisco estuary.

A-13

Benthic microalgal production under vascular plant canopies in tidal marshes can be quite high; in the relatively open canopies of some southern California marshes, for example, benthic primary productivity is similar to that of the vascular plant overstory (Zedler 1982; but see discussion in previous section regarding difficulties with vascular plant production estimates). In any case, existing studies do not permit a justifiable distinction between the levels of tidal flat and tidal marsh benthic production. Measurements from both habitat types span the entire range.

It remains to decide on the habitat area -- including both tidal flat and tidal marsh -- suitable for benthic production. If we wish to remain consistent with the simplifications introduced for estimating phytoplankton production, then we must accept as suitable all intertidal areas extending down to a depth of Z_p below MTL. The assumption is that, as for phytoplankton, benthic microalgae lying below the mean 1% surface light level do not receive sufficient insolation for sustained growth. Although benthic chlorophyll a may indeed be found on deeper sediments (Thompson et al. 1981), it could very well derive from the settling of planktonic forms. The latter may sometimes dominate not only the benthic microalgal biomass, but also the total biomass of microalgae both on the sediments and in the water column. Settled planktonic algae are an important contribution to the benthic microalgal biomass of Suisun Bay, for example, probably as a result of selective accumulation in the null zone (Cloern et al. 1985). Thus, the presence of chlorophyll in deep sediments is not necessarily evidence for in situ growth below Z_p. The upper boundary for the estimate of habitat area is MHHW, by necessity: The hypsometric information extends no further than this tidal datum. Some systematic error may be introduced by the exclusion of high marsh above MHHW -- and perhaps even some tidal flat area -- but most salt marsh above MHHW has disappeared (ABAG 1989).

The entire area from MHHW to a depth of Z_p below MTL was first estimated for each subembayment, using the hypsometric curve for MLLW (Fig. A.2), the areas at MTL and MHHW (Table A.2), and the value of Z_p for each subembayment. As in the calculations of phytoplankton production, linear interpolation was used to extend the hypsometric curves to include MTL and MHHW. The area was not corrected for slope, a relatively insignificant source of error (Fig. A.2). Using an areal production value of 120 g C m^{-2} yr^{-1}, the resulting benthic primary productivity estimates for the subembayments are (10^9 g C yr^{-1}):

SB	36
CB	11
SP	19
SU	6.9
SF	73

Recall that these subembayment estimates have a range of about ±60% due to uncertainty in the mean areal production estimate alone. Additional uncertainties arise from the simplifying assumptions used. The choice of mean photic zone depth is especially critical because of the sensitivity of estimated habitat area to this choice. For example, the value for Central Bay may appear rather high, in view of the steep topography and relatively small intertidal habitat. The

high value is due to its relative clarity and an assumed shoal $Z_p = 3.1$ m (Sec. A.2.1), which could be revised downward if shoal clarity is found to be less than channel clarity.

Further on, we will take the point of view that tidal marsh productivity, including the benthic microalgal component, is an allochthonous contribution to the open water-intertidal mudflat system. In that case, the contribution from tidal marsh benthic microalgae would be accounted for in the total tidal marsh export. The residual amounts contributed only by subtidal areas and intertidal mudflats can be estimated if we first subtract the amounts attributable to tidal marsh habitat using NWI map data for 1985. Once again, we assume that the small amount of Central Bay tidal marsh habitat can be ignored. The resulting benthic productivity values for open water and intertidal mud flats are (10^9 g C yr^{-1}):

SB	32
CB	11
SP	12
SU	1.7
SF	57

Together with the original estimates that included tidal marsh habitat, these estimates demonstrate that a substantial part of total benthic microalgal production may take place on tidal marsh sediments.

Note that these estimates are based on photic zone depths in 1980, with a correction for tidal marsh area from the 1985 NWI data. In the case of South Bay, net tidal marsh area changed little since 1958 -- the most recent NWI analysis prior to 1985 (ABAG 1989) -- and the South Bay estimate thus can be considered valid for 1980. The Central Bay estimate is also applicable to 1980, as Central Bay needed no correction for tidal marsh area. The 1958 NWI data has not been digitized for San Pablo or Suisun bays, however, so we must assume that marsh areas were essentially the same in 1980 and 1985 in order to apply the above estimates to 1980.

A.2.4 Seagrasses

Eelgrass (*Zostera marina*) is usually the dominant seagrass species in temperate estuaries of both the Atlantic and Pacific coasts of the U.S. and, indeed, appears to be the only seagrass of significance in the San Francisco estuary (Wyllie Echeverria and Rutten 1989). Its actual distribution in the Bay is limited, however, covering a total of only 128 ha, on the basis of a 1987 survey. Most of the eelgrass is found in Central Bay, which has 17 separate stands totalling 53 ha. San Pablo Bay has a single stand of 50 ha directly north of Point San Pablo and South Bay has a few stands totalling 25 ha in the vicinity of Alameda. An additional patch less than 1 ha in area is located at Coyote Point near San Mateo.

No productivity measurements have been made for these eelgrass stands. Values reported in the literature cover a wide range, from as little as 58 to as much as 1500 g C m^{-2} yr^{-1} (Mann 1972), including significant contributions from below-ground rhizome growth (Rasmussen 1973) and epiphytes (Penhale 1977). Most temperate eelgrass communities have productivities between approximately 100 and 500 g C m^{-2} yr^{-1}, including those of the subtidal Pacific Coast (Phillips 1974). Using a mean value of 300 g C m^{-2} yr^{-1}, the estimated values of seagrass productivity for the major subembayments are as follows (10^9 g C yr^{-1}):

SB	0.075
CB	0.16
SP	0.15
SU	none
SF	0.38

As implied in the above discussion, these estimated productivities have a range of $\pm 70\%$ due to uncertainty in the mean productivity value alone. Also, as the San Francisco estuary stands consist mostly of clumps rather than dense meadows, the actual productivity values may be in the lower part of the reported range for temperate eelgrass communities.

During typical winters, the northernmost stand in San Pablo Bay is subjected to salinities as low as 6 ^{o}/oo (Conomos et al. 1985), which may represent the low end of the salinity range for *Zostera* (Rasmussen 1973). This could be construed as evidence that low salinity prevents penetration further northward in the estuary. On the other hand, light availability is usually a critical factor determining seagrass distribution in turbid environments (e.g., Wetzel and Penhale 1983), and winter turbidity is often at a maximum north of the eelgrass beds (Conomos et al. 1985). The interpretation is further complicated by the relative absence of beds in the upper South Bay, where -- based on the location of beds elsewhere in the estuary -- the waters fall clearly within the salinity and turbidity range of eelgrass. Substrate, pollutants or the vagaries of colonization and extinction could conceivably have a role. Unfortunately, the absence of any historical data on seagrass communities precludes a search for environmental correlates of distributional change. Further, the information on current beds includes only the horizontal spatial boundaries. An unequivocal explanation of eelgrass distribution is thus not possible at this time.

A.2.5 Macroalgae

Most macroalgae in the estuary are restricted to Central Bay (Silva 1979; Josselyn and West 1985), although colonies do extend down into the southern part of South Bay and through the Carquinez Straits into Suisun Bay. Changes in percent cover of macroalgae have been followed on a seasonal and interannual basis at several sites, but no attempt has been made to assess the total standing crop in any of the major subembayments. The presence of numerous individual colonies of varying dimensions and depth render this task virtually impossible. The

patchy nature of macroalgal distribution reflects both the availability of suitable substrate -- particularly solid substrate such as rocks, pilings, and shells -- and the mobility of drift communities floating along the estuary bottom. This same substrate dependence, however, limits total macroalgae coverage on an estuary-wide basis. Thus, despite the fact that macroalgae have a capacity for high productivity in the estuary (Shellem and Josselyn 1982), their contribution to annual primary production is probably not significant (M. Josselyn 1990, pers. comm.). Actual contributions to individual subembayments are unknown, however.

Although macroalgae are of little importance to the estuary-wide carbon budget, they can form nuisance blooms of local significance. In South Bay, drift macroalgae can form unsightly, noxious accumulations along Alameda (Horne and Nonomura 1976). Decaying *Polysiphonia* blooms can smother benthic communities and alter the local benthic environment (Nichols 1979). In Central Bay, the green macroalgae *Ulva* and *Enteromorpha* attained dense accumulations off Albany in past summers (Bain et al. 1968); a nearby sewage treatment plant and the configuration of the basin were implicated. In San Pablo Bay, a bloom of *Cladophora* clogged cooling water intake pipes in 1979 (California Legislature 1979). These macroalgal blooms can disrupt recreational (beaches), industrial (cooling water) and food web (benthos) activities, and the possibility of increased bloom frequency in the future cannot be dismissed. Accordingly, the factors responsible for their occurrence should be of some concern. In San Pablo Bay, the blooms have been attributed to the coincidence of optimal light, temperature, salinity and tidal conditions (Josselyn and West 1985), but current understanding is insufficient to make reliable forecasts.

A.2.6 Other Autochthonous Sources

Photosynthetic bacteria inhabit areas where both light and reduced sulfur in the form of H_2S are available, usually on anoxic sediments where S^{2-} has been produced through dissimilatory reduction. In these circumstances, H_2S is used as an electron acceptor in photosynthesis, in contrast to the use of H_2O by conventional plants growing under aerobic conditions. The photosynthetic production is a true contribution to the organic carbon budget, although any energy subsidy arising from the use of locally-produced H_2S should be discounted. In any case, the habitat available to photosynthetic bacteria is a subset of the area for benthic microalgal production. As the latter was estimated on the basis of mean productivity and habitat area, the contribution of photosynthetic bacteria was included implicitly. It is possible that the productivity values used are not characteristic of photosynthetic bacteria in the Bay, but at least casual observation indicates that they occupy little area outside of the salt-evaporation ponds, which are essentially isolated from Bay waters (Nichols and Pamatmat 1988).

Epiphytic algae, mainly diatoms, are potentially large contributors to estuarine production, almost 10% of total primary production for some estuaries (Penhale and Smith 1977). They attach to submerged parts of vascular plants, macroalgae and seagrasses. Epiphytic production does not, however, alter the above estimated autochthonous contributions to the organic carbon pool of the Bay. In the case of tidal marsh vascular plants, for example, any contribution by

epiphytic growth was accounted for implicitly by the method used, namely, harvest of total biomass. Conclusions about macroalgal production will not be changed by including consideration of epiphytic growth: The lack of macroalgal significance is based on inadequate habitat area, not on low productivity. Finally, the range of seagrass productivities was also based on measures (^{14}C uptake, O_2 production, biomass changes) that implicitly included epiphyte production. In any case, epiphytic production is usually at the expense of the host plant, due to competition for light or nutrients (e.g., Phillips et al. 1978); epiphytes thus may result in a partition of production rather than a change in the total.

A.3 ALLOCHTHONOUS CARBON SOURCES

A.3.1 Delta outflow

The potential significance of Sacramento and San Joaquin River loading of organic carbon can be appreciated by noting that Delta outflow has recently ranged from 3.1 (1976-77) to 79 (1982-83) km^3 yr^{-1}, while the entire Bay has a MLLW volume of only 5.5 km^3. Schemel (1984) has compiled the only data set that bears directly on this question. Based on biweekly flow-weighted measurements of DOC at Rio Vista during 1980, Schemel (1984) estimated the Sacramento River flow of DOC to be 150 x 10^9 g yr^{-1}, with a mean annual flow-weighted DOC concentration of 5.0 mg l^{-1}.

POC data were collected only from April through December, so an estimate of annual POC transport requires additional assumptions. As there was no apparent seasonal trend in the ratio POC:DOC, based on the 9 months of overlapping data, the mean of this ratio -- 0.10 ± 0.02 (SE) -- was used to estimate an annual POC load of 15 x 10^9 g yr^{-1}. The corresponding annual mean flow-weighted POC concentration was 0.50 mg l^{-1}. The POC:DOC ratio could be seriously biased by the absence of January-March data, as 65% of annual river discharge took place during this period. Schemel (1984) pointed out that, even for the April-December period, actual POC:DOC ratios were probably higher, as samples were taken from near the surface and the ratio probably increased with depth. Peterson (1979), for example, estimated a POC load of 99 x 10^9 g yr^{-1}, using a POC:sediment ratio of 3%. Even if a ratio of 1% is used -- more typical of surface sediments deposited within the Bay (Thomson-Becker and Luoma 1985) -- the resulting POC load is twice the amount estimated from Schemel's (1984) surface samples.

Based on data for chlorophyll and its degradation products, much of this POC appears to be river-borne phytoplankton and phytoplankton-derived detritus. Chlorophyll measurements of near-surface samples at Rio Vista were aggregated by month (and interpolated for the few months where no chlorophyll measurements were collected). The data were combined with river flow measurements and an assumed C:Chl a ratio of 50 to arrive at a POC flux of 6 x 10^9 g C yr^{-1} associated with chlorophyll a. Pheopigments averaged 50% of chlorophyll a at Rio Vista during 1980 (Ball 1987a, Fig. 3b), suggesting a POC flux totalling 9 x 10^9 g C yr^{-1} for both phytoplankton and phytoplankton-derived detritus, or about 60% of the measured POC flux. Spiker and Schemel (1979) found that the stable isotope composition of POC just upstream of Suisun Bay was characteristic of riverine phytoplankton, not of land plants, a result that is consistent with the estimates presented here. Also, as pointed out by Ball (1987a), phytoplankton blooms in the western Delta are often carried into Suisun Bay when flows exceed 300 m^3 s^{-1}.

Because the Sacramento River contributed 76% of Delta inflow and an even larger fraction of Delta outflow, the composition of the Delta outflow was probably similar to the composition of the river (Schemel 1984). In the absence of adequate organic carbon measurements for the San Joaquin and east side rivers, the annual load of TOC into Suisun Bay can be estimated by multiplying Sacramento River transport by the ratio of Delta outflow to Sacramento River flow,

a factor of 1.08 in 1980. Summing the estimates for DOC and POC, the 1980 TOC load into Suisun Bay was about 180×10^9 g yr^{-1}, based on the data set of Schemel (1984). Recalling that more representative sampling of the vertical POC distribution could result in an upward revision of this estimate, $150\text{-}250 \times 10^9$ g yr^{-1} may be taken as the range of uncertainty.

All allochthonous sources, such as riverine loading, are capable in principle of supplying substrate for chemoautotrophy. Chemoautotrophic bacteria obtain their carbon from CO_2 but their energy from reduced inorganic substances, including nitrogen and sulfur species, Fe^{+2} and H_2. *Nitrosomonas* and *Nitrobacter*, for example, oxidize NH_3 and NO_2^-, respectively, in the process known as nitrification. The carbon incorporation represents a true addition to the organic carbon pool of the estuary, as long as the substrate originates outside the estuary. In the case of Delta discharge, the only river-borne substrate of any magnitude appears to be NH_3. Direct measurements of nitrification cannot assess the importance of allochthonous contributions, as nitrification assays include substrate produced by ammonification of organic matter within the estuary. External loading, however, establishes an upper limit of nitrification contributions to the food web. Approximately 2×10^9 g yr^{-1} NH_3-N is contributed by Delta outflow (estimated from the data of D.H. Peterson et al. 1985). On the other hand, 35 mol of NH_3 are required for each mol of CO_2 fixed (Atlas and Bartha 1987). The entire riverine NH_3 load can thus support a maximum of only 0.05×10^9 g C yr^{-1} chemoautotrophic production. The actual amount utilized in nitrification is undoubtedly much lower, considering the possibility for outwelling (i.e., release through the Golden Gate) and chemical oxidation. Uptake by phytoplankton is also a likely fate for much of this NH_3 loading (Peterson 1979), but this could actually be considered an energy subsidy in the sense that it offsets energy requirements for reduction of NO_3^-, which would otherwise need to be assimilated.

The consequences for the food web of riverine organic carbon may be far less than implied by the high loading values. River-borne organic carbon arises from several sources, including phytoplankton, aquatic macrophytes, litter from terrestrial vegetation, leaching of soils, sewage effluent, and so on. The lability of this detritus -- that is, the ease with which it can be utilized -- is highly variable and is often characteristic of the source. Municipal sewage effluent will degrade relatively quickly, for example, while humic substances formed in the breakdown of terrestrial plant material are relatively long-lived (Wetzel 1975 provides a detailed discussion of detritus and decomposition).

Refractory humic substances often constitute more than 90% of the DOC in river water (Reuter 1977), suggesting that a large fraction of this DOC may pass through the estuary unchanged, not participating in the estuarine carbon cycle. Although the breakdown times of humic-rich riverine DOC may be much shorter than previously thought (Keiber et al. 1990), they are still too long for these substances to be a source of organic carbon to the estuarine food web.

In the case of POC, refractory materials may be avoided by consumers or, even if ingested, may contribute little to energy needs. As with refractory DOC, microbial transformation may be required before refractory POC can enter the food web. On a global basis, typically about 35% of riverine POC consists of highly labile materials such as sugars and

amino acids (Ittekot 1988). Depending on the hydraulic residence time within the estuary, less labile material also may become available. The exact amount depends both on the nature of the river-borne material and the hydraulic residence time in the estuary.

Bacterial processes may play an essential intermediary role between allochthonous sources of organic matter and larger planktonic or benthic invertebrates. Riverine phytoplankton, for example, must undergo osmotic stress within the vicinity of the entrapment zone, probably liberating organic material for bacterial processing. Also, detrital material from upstream may be colonized by bacteria and rendered more desirable and nutritious for consumers such as *Neomysis mercedis*, which often has abundant detritus in the gut (Kost and Knight 1975).

No studies appear to have been conducted explicitly on the suitability of organic carbon from Delta discharge as a food for primary consumers, but some pertinent indirect evidence exists. Five-day Biochemical Oxygen Demand (BOD_5) was measured at several Department of Water Resources (DWR) stations along the Sacramento River between Rio Vista and Chipps Island from 1968 to 1977. The sites (and periods of record) were as follows: below the Rio Vista Bridge (D24, 1968-1970); at Emmaton (D22, 1968-1970); above Point Sacramento (D4, 1973-1977); and at Chipps Island (D10, 1968-1970, 1973-1977). Data were collected approximately monthly during the indicated periods. No differences in the mean values could be found among sites for the periods 1968-1970 (D24, D22, D10) or 1973-1977 (D4, D10). No trend in the annual mean could be detected at Chipps Island, the only station for which a long record existed. The mean BOD_5 value was 1.3 ± 0.1 (SE) mg l^{-1}. If we assume a $C:O_2$ molar ratio of 1, this level of BOD_5 corresponds to 0.49 mg l^{-1} organic carbon, which can be considered an indication of " readily available" organic carbon. The lack of any long-term trend suggests that we might apply this mean to 1980 as well. Recall that measured TOC averaged 5.5 mg l^{-1} at Rio Vista in 1980, implying that, of the total 180×10^9 g yr^{-1}, at least 16×10^9 g C yr^{-1} -- approximately 10% -- was readily available for assimilation and metabolism by bacteria and perhaps higher organisms. This value is consistent with the results from global studies quoted above.

It is useful to examine the magnitude of BOD_5 loading from Central Valley point source dischargers. A minimum estimate for the early 1970s -- when secondary treatment was beginning to expand -- as well as for 1979, has been assembled by Hansen (1982). The 1979 values amount to 3.2×10^9 g BOD_5 yr^{-1}, equivalent to a TOC of 1.2×10^9 g C yr^{-1}, or 1.6×10^9 g C yr^{-1} if we use convert the BOD_5 to ultimate BOD using typical values for sewage (Sec. A.3.3). The actual values may be higher than this minimum estimate. On the other hand, much of this material may already be oxidized before it reaches the Bay. In any case, there is no evidence that point source discharge upstream of Suisun Bay is a major component of TOC loading from Delta outflow.

A.3.2 Tidal marsh export

An alternative way to assess the influence of marsh productivity is to examine only the organic carbon export. Whatever the production level, some will be utilized by consumers within the tidal marsh habitat itself and some will be exported to other habitats in contact with the marsh through water transport. The magnitude of this export is of some interest, as many consumer organisms are excluded from tidal marsh by their environmental needs. For these organisms, it is preferable to consider tidal marsh production as an allochthonous contribution of organic matter. No relevant measurements of organic carbon flux between tidal marsh and other habitats of the Bay have been published, although some studies exist on nitrogen exchange (Bucholz 1982). In the absence of any direct measurements, we must turn to results from other estuaries.

Nixon (1980) characterizes the magnitude of TOC flux from tidal marsh as lying in the range of 100-200 g C m^{-2} yr^{-1}, based on data from 5 studies. Four of the marshes actually had values lying within an unusually small range of 100-165 g C m^{-2} yr^{-1}; the remaining marsh was a net importer of TOC, but this appeared to be attributable to intense filter feeding of a mussel bed near the mouth of the tidal inlet. The agreement among the sites is quite remarkable, in view of the uncertainties in measuring water exchange (Nixon 1980) and other possible errors due to the highly intermittent nature of major transport events and an unmeasured but possibly significant bedload transport (e.g., Odum et al. 1979). The number of cases is small, however, and the agreement may be fortuitous. For example, indirect estimates of TOC export were about 400 g C m^{-2} yr^{-1} for two studies of Barataria Bay, Louisiana (Day et al. 1973; Kirby and Gosselink 1976), as well as for Sapelo Island, Georgia (Teal 1962). Exports of more than 400 g C m^{-2} yr^{-1} were estimated for the North Inlet in South Carolina (Kjerfve and McKellar 1980; Chrzanowski et al. 1983). Modeling studies based on data for *Spartina anglica* stands in the Severn Estuary also suggest exports of more than 400 g C m^{-2} yr^{-1} (Randerson 1986). In contrast, Borey et al. (1983) estimated an export flux of only 20-30 g C m^{-2} yr^{-1} for Coon Creek, Texas. Roman and Daiber (1989) recently estimated a flux of 110 g C m^{-2} yr^{-1} for Canary Creek, Delaware -- more consistent with a range of 100-200 -- but transport by coastal storms was not included. To summarize, the uncertainty range for TOC export fluxes extends from negative values up to about three times the "typical" estimate of 150 g C m^{-2} yr^{-1} implied by Nixon (1980).

The estimates are further complicated by the important role of reduced sulfur compounds in marsh metabolism. Anaerobic decomposition in which SO_4^{2-} is the major electron acceptor is the dominant decomposition pathway in at least some saltwater marshes The energy released during anaerobic respiration is only about 25% of that for aerobic respiration; the remainder is stored in reduced sulfur compounds such as H_2S, which may be subsequently utilized as an energy source by various chemoautotrophic organisms in the marsh or adjoining habitat. In the Great Sippewissett marsh, about 75% of the annual energy export was actually in the form of reduced sulfur compounds (Howarth and Teal 1980; Peterson et al. 1983). Although sulfate reducers are definitely active in the San Francisco estuary (Oremland and Silverman 1979; Oremland et al. 1982), the allochthonous contribution of reduced sulfur compounds from tidal

marshes remains unknown. Export of reduced sulfur would, however, increase the allochthonous energy contributions of tidal marsh beyond that estimated on the basis of organic carbon export alone. At the Great Sippewissett, for example, if transformed into organic carbon with 25% efficiency, reduced sulfur export is equivalent to almost 200 g C m^{-2} yr^{-1}.

As in the case of river-borne organic carbon, the issue of *availability* arises for tidal marsh export. The availability of exported material is a complex and controversial subject (reviewed by Valiela 1984; Mitsch and Gosselink 1986; and especially Mann 1988), and the quantitative significance of this issue for the San Francisco estuary is unknown.

Bearing these caveats in mind, a mean export value of 150 g C m^{-2} yr^{-1} results in the following annual mass exports for the tidal marshes of each subembayment, based on the NWI habitat maps for 1985 (10^9 g C yr^{-1}):

```
SB   5.2
CB   0
SP   9.8
SU   6.4
-------------
SF  21
```

As discussed in the context of benthic microalgal productivity (Sec. A.2.3), the South and Central bay estimates can be applied to 1980 as well. For the other two subembayments, it is necessary to assume that tidal marsh areas changed little between 1980 and 1985.

A.3.3 Point sources

The term "point source" usually refers to a source of material load to the estuary that enters at a discrete location and can be identified as the waste stream of an individual discharger. An example is the discharge from a municipal wastewater treatment plant. Point source dischargers in the Bay area are regulated by the California Regional Water Quality Control Board, San Francisco Bay Region (CRWQCB-SFBR), which compiles the monitoring data of individual dischargers. Gunther et al. (1987) describe the state of this data set in some detail. At the end of 1986, 205 permits were in effect for point-source discharges to San Francisco Bay, although not all were active.

Organic carbon data (i.e., TOC, DOC, and POC) are not part of the required monitoring program for point sources. As a result, we are compelled to make inferences about carbon loading from the routine measurements of Biochemical Oxygen Demand (BOD). BOD values correspond to the metabolizable fraction of the organic carbon load, and thus may be more germane than TOC to the issue of energy supply to the food web. In order to compare with the contributions from other sources, however, it is necessary to attempt some kind of conversion to our common currency, namely, organic carbon. Although interchangeability of TOC and BOD

is often assumed in mathematical models of biological oxidation, experimental and field studies suggest that the TOC:BOD ratio is highly variable (e.g., Kim 1987; Pinter et al. 1980). This lack of correspondence is not surprising, considering the variety of carbon sources entering the waste stream, particularly when industrial effluent or urban runoff are combined with domestic waste. The theoretical TOC:BOD ratio depends not only on the material undergoing decomposition, but also on the degree of treatment; the ratio of refractory to labile organic materials increases in treatment, resulting in a progressive increase in the TOC:BOD ratio (Tittizer 1978).

Although it is difficult to specify a priori a range for TOC:BOD, we can arrive at a lower limit on theoretical grounds. Let us assume that the sewage has a respiratory coefficient -- that is, $C:O_2$ molar ratio -- of 1, which is typical of carbohydrates and even proteins before nitrification of NH_3. This may be appropriate for San Francisco Bay, in which about 90% of the BOD loading is due to municipal and only 10% to industrial sources (T. Wu 1990, pers. comm.). A respiratory coefficient of 1 implies a TOC:BOD mass ratio of 0.38. Dischargers usually report BOD_5, which is typically two-thirds of the ultimate BOD in domestic sewage (Warren 1971). The $TOC:BOD_5$ ratio is thus 0.57. This value would be reduced if some of the ammonia released were oxidized as well. In the case of phytoplankton, for example, where the C:N molar ratio is typically 16, the complete nitrification of NH_3 to NO_3^- would result in a $TOC:BOD_5$ of 0.43. As nitrification facilities, however, are not integrated into some of the larger treatment plants in the Bay area -- for example, the East Bay Municipal Utility District (EBMUD) plant -- most sewage nitrogen reaches the Bay as NH_3 (Conomos et al. 1979, Table 3) and an intermediate TOC:BOD ratio is probably appropriate for proteinaceous material. Moreover, although many of the fatty substances in municipal sewage are removed during primary treatment, a colloidal suspension of fats may survive even secondary treatment, as observed at the EBMUD plant (W. Hellier 1990, pers. comm.); these fats would also tend to decrease the TOC:BOD ratio. Accordingly, we choose here a mass ratio of 0.5, somewhat lower than the value corresponding to a respiratory coefficient of unity; the amount of metabolically available TOC is thus assumed to be at least half the mass of the BOD load. In fact, a range of 0.5 to 1 is commonly encountered for municipal raw sewage and primary effluent (e.g., Meron 1970; Iskandar 1978), where one would expect the lowest values. A ratio of 0.5 thus seems to be a reasonable minimum for municipal waste, based on both theoretical and empirical evidence; the high end of the range, however, is uncertain.

The CRWQCB-SFBR has compiled municipal BOD_5 loadings to San Francisco Bay for the period 1955-1985, by subembayment (CRWQCB-SFBR 1987). The estimated minimum TOC loadings in 1980, assuming a $TOC:BOD_5$ of 0.5, are (10^9 g C yr^{-1}):

SB 6.6
CB 4.7
SP 0.18
SU 1.5
――――――――――
SF 13

Industrial discharge, not included in the above loading estimates, accounted for an additional 5% of BOD_5 load, at least in 1985 (T. Wu, pers. comm. 1990).

Although EBMUD discharges into a region considered part of Central Bay according to the AHI segmentation scheme, the CRWQCB-SFBR classifies EBMUD as a South Bay discharger. EBMUD had an average flow of 120×10^9 l yr^{-1} during the period 1984-1986 (Gunther et al. 1987), which is about 20% of the total South Bay point source discharge for 1985 (CRWQCB-SFBR). Thus, the South Bay value should be decreased somewhat and the Central Bay value increased by the same amount. As will become clear, however, omission of this adjustment does not affect any conclusions.

It is also of interest to calculate the implied TOC concentrations in waste discharge given the estimated "available" TOC loads and the waste flow for each subembayment. Estimates were made for 1985 -- year of the most recent CRWQCB-SFBR compilation -- in order to compare with recent actual TOC measurements. These implied TOC concentrations are (mg l^{-1}):

```
SB   4.8
CB  12
SP   9.3
SU  10
_____

SF   6.1
```

Some data are available for effluent TOC concentrations from the San Jose/Santa Clara Water Pollution Control Plant, which is the single largest discharger in the South Bay. In autumn of 1989, samples for TOC analysis were collected from Artesian Slough, which receives discharge from the plant (T. Grovhoug 1990, pers. comm.). The low salinities of these samples indicated that they were, indeed, mostly sewage effluent, largely undiluted with Bay water. The samples contained 7.4-8.4 mg l^{-1} TOC. Certain effluents have much higher TOC concentrations. For example, based on daily TOC measurements from 12 June 1989 through 1 June 1990 (W. Hellier 1990, pers. comm.), the mean effluent TOC for EBMUD is 30 mg l^{-1}. Although these data are consistent with the estimates of 4.8 and 9.3 mg l^{-1}, respectively, for "available" TOC, they do raise the possibility of much higher values. A meaningful uncertainty range cannot be given, however.

As in the case of river-borne NH_3, sewage NH_3 must be considered a potential fuel for chemoautotrophic contributions to the organic carbon pool. The maximum rates of nitrification in estuaries have been measured, in fact, directly beneath sewage outfalls, where high NH_3 and sufficient O_2 occur (Billen 1975; Vincent and Downes 1981). Point source waste loads of NH_3-N can be estimated by combining NH_3:BOD ratios for 1975 waste loads in each subembayment (Peterson 1979) with the 1980 BOD data (CRWQCB-SFBR 1987). The resulting loads total 3.3×10^9 g yr^{-1} NH_3-N, similar to the river-borne load and equally unimportant.

A.3.4 Runoff

The category of runoff is defined to be all loads to the Bay carried by inflowing water that are not included in Delta outflow, tidal marsh export, or point sources. This category is not equivalent to the load contributed by local rivers and creeks, as they may also carry sewage (e.g., Coyote Ck.) and tidal marsh contributions (e.g., Petaluma R.). In fact, summer inflow in the South Bay may be largely due to treated wastewater effluent. The loading from runoff must therefore be assessed through indirect methods.

Russell et al. (1982) tabulated BOD_5 loading from several sources, including surface runoff, for 1978. For the entire Bay, the runoff BOD_5 was 6.7×10^9 g yr^{-1}, which, according to our previous discussion on point sources, may be equivalent to at least 3.4×10^9 g C yr^{-1}. The amounts were not partitioned among the various subembayments and the basis for the estimates was not explicitly detailed.

An alternative estimate can be made by examining typical TOC concentrations in runoff water. Silverman et al. (1985) measured TOC at 15 runoff stations over a 12-month period (1984-1985). The mean value was 8.1 ± 0.9 (SE) mg l^{-1}; variability due to storms and land use was small. A more recent study of nonpoint sources in the San Pablo Reservoir watershed similarly found a TOC concentration of 8-10 mg l^{-1}, regardless of whether the land use was residential, commercial or open space (Smith 1989). Runoff volumes for 1977, 1981, and 1982 were assessed by Gunther et al. (1987). Estimates were based on precipitation data from the National Climatic Data Center (NCDC) and runoff coefficients developed by the National Oceanographic and Atmospheric Administration (NOAA) for different land use types. The runoff estimates treat Central and San Pablo bays as a unit, and we are consequently forced to do the same here for organic carbon loading. If we assume that 8 mg l^{-1} is a characteristic TOC concentration in runoff and use runoff volumes for 1981, then the corresponding loadings are (10^9 g C yr^{-1}):

```
SB   3.1   (0.96-4.8)
CB   -
SP   1.8   (0.80-2.4)
SU   0.64  (0.29-0.80)
_____
SF   5.5   (2.0-8.0)
```

The values in parentheses represent the range based on estimated runoff volumes for a dry year (1977) and a wet year (1982). The range is clearly consistent with the values based on the tabulation by Russell et al. (1982). Although runoff volumes were not estimated for 1980, it was a precipitation year intermediate between 1981 and 1982. The loading from runoff probably was also intermediate between the values for 1981 and 1982. The loading values for 1980 are therefore estimated as 4×10^9 g C yr^{-1} for South Bay, 2×10^9 for Central plus San Pablo bays, and 0.7×10^9 for Suisun Bay.

A.3.5 Other allochthonous sources

A variety of other possible allochthonous sources can be entertained. Russell et al. (1982), for example, estimated an aerial fallout of 1.8×10^9 g BOD_5 yr^{-1} to the surface of the Bay in 1978, implying atmospheric deposition of at least 0.90×10^9 g TOC yr^{-1}. On the basis of data for Chesapeake Bay, Gunther et al. (1987) extrapolated a total hydrocarbon deposition of only 0.045×10^9 g yr^{-1} to San Francisco Bay.

Oil spills are also common in the Bay, although the mass loading from spills was estimated to be only about 0.073×10^9 g yr^{-1} of petroleum hydrocarbons in 1986 (Gunther et al. 1987) and presumably even less in terms of TOC. A large interannual variability in spills would not be surprising, but annual spillage during the period 1984-1986 was quite consistent at 0.09 ± 0.01 (SE) $\times 10^9$ g yr-1 petroleum hydrocarbons.

Groundwater loading appears to be a completely unknown source. Russell et al. (1982) did not include groundwater among the significant freshwater sources to San Francisco Bay (but there was no explicit justification). If groundwater flow is indeed minor compared to, for example, runoff, then organic carbon loading from groundwater is probably negligible as well; there is no reason to expect much higher concentrations of organic carbon in groundwater than in runoff.

A.4 EXCHANGE PROCESSES

A.4.1 Circulation and mixing

Exchange processes include forms of transport that can transfer organic carbon both into and out of the region of interest, that is, San Francisco Bay or its major subembayments. We could break down the net flux into the sum of a source and a sink and thus avoid the creation of this intermediate category of processes. But when the source and sink are so closely linked -- especially in the case of turbulent mixing across boundaries -- both efficiency and understanding are better served by considering the two fluxes together.

Physical exchange processes have a great potential for modifying the carbon budget. At the junction between adjoining subembayments, as well as at the Golden Gate, water moves both seaward and landward due to a number of different forces, including tides, Delta discharge, density gradients, and the wind. As Delta discharge greatly exceeds Bay evaporation on an annual basis, the net yearly flux of water is, of course, in a seaward direction, but there is no a priori reason to conclude the same for DOC and POC. In the Grevelingen estuary, for example, import from the North Sea accounts for at least half of the POC sources (Wolff 1977). The actual net fluxes depend not only on the direction and intensity of advective and diffusive transport, but also on the distribution of organic carbon in the plane of the interface between estuary and ocean.

Conomos (1979), Walters et al. (1985), and Smith (1987) have reviewed mixing and circulation processes in the estuary. The understanding of hydrodynamic behavior in the Bay is considerable. Nonetheless, the magnitude of organic carbon exchange cannot be estimated to any useful degree of certainty, either between subembayments or through the Golden Gate. Little enough is known about the flux of a much-studied conserved quantity such as salinity (e.g., Walters et al. 1985). In the case of OC, we face additional difficulties due to the lack of data on spatial distribution. An inventory of STORET data, for example, performed in October 1989, yielded only 117 measurements of DOC and 506 measurements of TOC for the entire Bay-Delta region. More complete data are available for POC (Schemel and Dedini 1979), but, even so, sampling was confined to surface waters. In particular, the lack of vertically-averaged data for both carbon and velocity precludes estimation of mean advection of the mean organic carbon; the low frequency of measurements (viz., less than 1 per tidal cycle) prevents understanding of diffusive flux; and the lack of data on vertical distribution prevents assessment of net flux due to the estuarine circulation. All three processes can be significant for salt flux at the Golden Gate, for example.

Despite the inability to estimate exchange between subembayments or at the Golden Gate, some crude calculations can be used to illustrate the critical role of transport. First, we consider the ramifications of estuarine circulation on transport through the Golden Gate. Estuarine circulation induced by winter runoff causes a flow of bottom waters into the Bay from the coastal ocean, as clearly evidenced by long-term drifter movement (Conomos and Peterson

1977). Peterson (1979) estimated oxygen exchange due to this circulation by assuming an average nontidal flow landward of 5 km d^{-1} and seaward of 6 km d^{-1} (Conomos 1975), each characterizing half the cross-sectional area at the Golden Gate. Based on the STORET data, the mean TOC value is 4.8 ± 0.2 (SE) mg l^{-1} for the Bay-Delta. If we assumed a TOC value of 5 mg l^{-1} for Central Bay and the flow rates used by Peterson (1979), the seaward losses would be 480 x 10^9 g yr^{-1}, larger than any of the source terms considered previously.

Given these seaward losses, the *net* flux depends on the concentration of TOC in inflowing bottom waters. These concentrations are unknown. But for illustrative purposes, let us compare the net fluxes through the Golden Gate for two different TOC concentrations in bottom waters: 4 and 8 mg l^{-1}. In the first case, the landward flux would be 320 x 10^9 g yr^{-1}, resulting in a net flux of 160 x 10^9 g yr^{-1} *seaward*; in the second case, the landward flux would be 640 x 10^9 g yr^{-1}, resulting in a net flux of 160 x 10^9 g yr^{-1} *landward*. Both fluxes have large ramifications -- but in opposite directions -- for the carbon budget for Central Bay, as well as for the entire Bay. Clearly, ocean-Bay exchange is capable, in principle, of drastically modifying supply and loss rates for the estuarine pool of organic carbon.

A similar argument can be made for the potential importance of diffusive flux. Longitudinal diffusion coefficients have been assessed by several investigators, with estimates falling in the approximate range of 0.1-1 x 10^6 cm^2 s^{-1} (Conomos 1979, Table 4) and decreasing toward the Golden Gate in both the northern and southern reaches. A diffusivity of 0.4 cm^2 s^{-1} and a gradient of 0.1 mg l^{-1} km^{-1} TOC through the Golden Gate would result in a flux of 11 x 10^9 g yr^{-1} due to mixing, comparable to estimates for benthic microalgal production in Central Bay. Peterson and his coworkers (Peterson et al. 1978; Peterson and Festa 1984) used a much higher mixing coefficient (4 x 10^6 cm^2 s^{-1}) in order to simulate silica and phytoplankton distributions. Clearly, diffusive as well as advective fluxes may transport significant amounts of TOC between ocean and Bay, as well as between subembayments.

Some comments also can be made on the direction of net transport. The POC measurements of Schemel and Dedini (1979) suggest a gradient downward toward the Golden Gate for the northern reach (seaward of the null zone) and southern reach during winter, at least for data averaged over several years (Conomos et al. 1979, Fig. 9). If these measurements were representative of the entire water column -- and not just the surface waters where the samples were collected -- then the diffusive transport of POC should be seaward from all subembayments in winter. Indeed, a decrease in POC from estuary to coastal sea is common (Head 1976). In summer, on the other hand, average values were approximately the same from northern San Pablo Bay to below the San Mateo Bridge, with no clear gradient. On an annual basis, sediment budgets suggest a net transport of sediments from South Bay (Krone 1979). Similarly, Conomos et al (1979) describe a net transport of South Bay sediment from inflows and bottom resuspension to Central Bay, where it is deposited or released to the ocean. The sediment data may be considered weak evidence for similar behavior of POC. The existing data thus support a net seaward transport of POC.

A.4.2 Dredging activity

Dredging and dredged material disposal -- arguably a form of biotic transport, but treated separately here -- results in the transport of large quantities of sediment within and between subembayments, and between Bay and ocean. Currently, four open water dredge disposal sites exist: Alcatraz, San Pablo Bay, Carquinez Strait, and Suisun Bay (AHI and PWA 1990). The Alcatraz site is the only one to which material is transported from another subembayment, primarily South Bay. AHI and PWA (1990) tabulated annual average Federal dredging for the period 1975-1985, when a mean of 0.97×10^6 m^3 was transported from South Bay to the Alcatraz site. A crude estimate of the organic carbon content can be determined by assuming a solids content of 34% (AHI and PWA 1990) and a mean TOC:dry wt. of 1.4% (Thomson-Becker and Luoma 1985). The implied movement of organic carbon amounts to 4.6 $\times 10^9$ g C yr^{-1} using these approximations. During 1986-1987, 38% of the dredging was generated by non-Federal projects (AHI and PWA 1990). If we apply this same value to the period 1975-1985, then the organic carbon transported between South and Central bays would increase to 7.4×10^9 g C yr^{-1}.

In view of the uncertainty in our assumptions, the transport could be considerably smaller or larger. The TOC data, for example, has an uncertainty range of 0.5-2% dry wt., and may also be spatially biased as samples were collected only from intertidal stations (Thomson-Becker and Luoma 1985). Furthermore, much of the material dumped at the Alcatraz site may consolidate and accumulate on the bottom. USCOE (cited by AHI and PWA 1990), for example, estimated that 38% of the material disposed at Alcatraz remained at that site as consolidated bottom material. A value of only 5×10^9 g C yr^{-1} is therefore used for 1980.

In San Pablo and Suisun bays, dredging activity results only in a redistribution of organic carbon, although the altered distribution may ultimately result in changes for other fluxes such as physical transport (AHI and PWA 1990).

A.4.3 Biotic Transport

Biotic transport, where it has been estimated quantitatively, almost always represents a net loss to the estuarine ecosystem. For example, Hopkinson and Day (1977) estimated a net faunal outmigration of 89 g dry wt. m^{-2} yr^{-1} for Barataria Basin, Louisiana. Similarly, Knox (1983) estimated a net migration loss of 4.5 g C m^{-2} yr^{-1} fish and 0.13 g C m^2 yr^{-1} birds from the Upper Waitemata Harbour, New Zealand. Almost no quantitative data are available regarding biotic transport for San Francisco Bay, but there is little reason to believe that this estuary is an exception.

The northern anchovy (*Engraulis mordax*) is probably the most abundant species in the Bay as a whole, and probably in each of the three seaward subembayments as well. Although capable of spawning in the Bay, most spawning may actually take place out of the Bay. If this is indeed the case, then the anchovy is more likely a sink than a source for the Bay organic carbon pool.

The same could be deduced about any marine migrant that is also a saltwater spawner, using the estuary only as a nursery.

The Pacific herring (*Clupea harengeus*), a marine migrant that is an estuarine spawner, provides one of the better-documented cases of biotic transport. Herring enter the Bay each year from late fall through winter to spawn along the western shores of Central Bay north of the Golden Gate. Although adults spend only a few months in the Bay, a large fraction of their biomass is deposited as eggs. Numbers have been increasing in recent years and the estimated 1989 population biomass was 71×10^9 g wet wt. (J. Spratt 1990, pers. comm.). Assuming that eggs constitute 22% of the biomass and that the C:wet wt. ratio is 0.15 for eggs, the 1989 population was carrying 2.3×10^9 g C of eggs. Up to 15% of the estimated population size can be harvested; the remaining fish and eggs are subject to intense predation by other fish, gulls, and sea lions. The young from surviving eggs feed in the Bay -- mostly Central and San Pablo bays -- for 9 months before moving out to sea. The herring migration could result in a net gain to the estuary only if the biomass of deposited eggs and mortality in the estuary exceeded the outmigration of surviving young and adults.

Certain anadromous species migrate from the sea through the estuary to upstream spawning areas. The adults die -- their carcasses may eventually contribute to riverine loading of organic carbon -- and the young move through the estuary back to sea. Some direct contributions to the estuarine organic carbon pool may occur through mortality during migration, but these are probably minor. For example, migrating chinook salmon (*Oncorhynchus tshawytscha*) number between approximately 70,000 and 500,000, with a typical wet weight of 5 kg. The equivalent organic carbon is only about 0.1×10^9 g C yr^{-1} (Gulland 1970), which would have a minor effect even if all of it ended up in the estuary. Similarly, the biomass of migrating American shad (*Alosa sapidissima*) is probably between 0.1 and 1×10^9 g C yr^{-1}.

Other anadromous fish feed and grow within the estuary, not simply using it as a migration route. These species, such as striped bass (*Morone saxatilis*), are most likely a sink, transporting the accumulated biomass upstream to spawn.

No basis appears to exist for assessing biotic transport due to marine mammals or waterfowl in the Bay. The migratory biomass of marine mammals and the consequent effect they can have on TOC transport is likely to be even less than for fish populations. As far as waterfowl are concerned, the Bay-Delta is part of the Pacific Flyway and millions of birds feed off of vegetation in the marshes. Their activity may very well increase the loading of organic carbon to estuarine waters. However, this contribution would fall into the category of tidal marsh export, not biotic transport, and presumably was included in the measurements from other estuaries on which we base our estimates of tidal marsh contributions.

A.5 ORGANIC CARBON SOURCES FOR INDIVIDUAL SUBEMBAYMENTS

A.5.1 Overview

A summary and comparison of the individual estimates for 1980 is informative, but a certain caution must always be borne in mind. Estimates for several processes that may be important -- benthic microalgal productivity and tidal marsh export, for example -- have a large range of uncertainty, perhaps as large as an order of magnitude, that is, a factor of $10^{\pm 0.5}$. The errors have been treated partially, but for the most part remain unquantified. Even when uncertainty ranges are specified, there is often no objective way to utilize them in comparing estimates. The probability of a given value within the uncertainty range is usually neither uniform nor Gaussian. Thus, the fact that two uncertainty ranges overlap implies that the two processes could be similar in magnitude, but indicates nothing regarding the likelihood. Nonetheless, these ranges do have value. First, when ranges for two processes truly do not overlap, we can conclude that the processes differ in magnitude. Second, uncertainty ranges make explicit the potential for error, even if the error cannot be specified quantitatively. The tendency to naively accept carbon budget estimates at face value is rampant in the scientific literature, leading to a premature acceptance of tenuous conclusions and poor management decisions. Finally, when uncertainty ranges are combined with the need for conservation of mass, analytical techniques can be used to determine if the underlying conceptual model and data are consistent (Klepper and Van de Kamer 1987). They also can be used to narrow the uncertainty ranges. This optimization approach requires estimates of all sources and sinks, something not possible within the constraints of the current report, but a worthy goal for the near future.

The estimates of the previous two sections provide some guidance as to conditions in 1980 (Table A.4). Several groups of processes can be distinguished, based on their percentage contribution to the known organic carbon sources of each subembayment, that is, excluding physical transport. Percentages were calculated under the assumption that only 10% of the TOC loading from Delta discharge is available (Sec. A.3.1). Sources other than Delta discharge were not corrected, due to the lack of data. However, the main sources in the Bay -- planktonic and benthic microalgal productivity -- are probably largely available to the food web, either through direct consumption or after transformation to detritus and bacterial biomass. It was thought that correction of the Delta loading alone, although seemingly inconsistent, would actually give a more accurate picture of food sources in the Bay than making uncertain assumptions about the availability of other sources, or making no adjustments at all:

(1) The first group consists of those processes that were almost definitely unimportant, based on their negligible contribution and a judgement that uncertainty ranges do not include nonnegligible contributions. This group includes seagrasses, photosynthetic bacteria, atmospheric deposition, spills, and runoff. They probably contributed a total of less than 10% in the case of each subembayment.

(2) The second group consists of processes that also appear to be insignificant, but the evidence is anecdotal and the conclusion less certain. This group includes macroalgae, groundwater, and biotic transport.

Table A.4
Organic carbon sources for San Francisco Bay and its major subembayments (10^{11} g C yr^{-1}).

Carbon sources	SB	CB	SP	SU	SF	Year
Autochthonous						
Phytoplankton	0.71	0.15	0.39	0.05	1.30	80
Benthic microalgae[a]	0.32	0.11	0.12	0.02	0.57	80,85
Seagrasses	0.00	0.00	0.00	0.00	0.01	87
Macroalgae	n.s.	n.s.	n.s.	n.s.	n.s.	–
Photosynthetic bacteria	n.s.	n.s.	n.s.	n.s.	n.s.	–
Allochthonous						
Delta discharge	0.00	0.00	0.00	1.80	1.80	80
Tidal marsh export	0.05	0.00	0.10	0.06	0.21	85
Point sources	0.07	0.05	0.00	0.02	0.13	80
Runoff[b]	0.04	–	0.02	0.01	0.07	80
Atmospheric deposition	0.00	0.00	0.00	0.00	0.01	78
Spills	0.00	0.00	0.00	0.00	0.00	86
Groundwater	n.s.	n.s.	n.s.	n.s.	n.s.	–
Transport						
Circulation and mixing	?	?	?	?	?	–
Dredging[c]	0.00	0.05	0.00	0.00	0.00	75–85
Biotic transport	n.s.	n.s.	n.s.	n.s.	n.s.	–

Notes: Tidal marsh habitat is external to the system boundaries under consideration. Where applicable, epiphyte production is implicitly included with host plant production. Estimates are for the indicated year only. The uncertainty in some of these estimates is considerable and the text must be consulted for essential details. N.s. = probably not significant, but no quantitative evidence.

[a]Intertidal habitat area based on 1985 data, subtidal on 1980 photic depth data.
[b]CB included with SP.
[c]Average for 1975-1985.

(3) A third category consists of processes that contributed at least 10% in at least one subembayment, but never more than 25%. This group includes tidal marsh export, point sources and dredging. These fluxes may have been significant secondary sources, but were probably not major sources, during 1980.

(4) The final group is composed of processes that were major sources (>25%) for at least one subembayment during 1980. Phytoplankton and Delta discharge belong to this category, and in fact each was the dominant source (>50%) for at least one subembayment. Benthic microalgal productivity was never dominant, but may have been a major source for South and Central bays. Physical transport may very well also be a member of this group.

The first two groups will be dropped from consideration in what follows. No evidence supports the notion that any of these processes are significant sources for the organic carbon pool, that they were notable in the past, or that they will be in the future (see Russell et al. 1982 on long-term trends in atmospheric deposition and runoff of BOD_5; and Silverman et al. 1985 regarding short-term trends in runoff of hydrocarbons). Even if all other sources in each subembayment were to drop by a factor of ten, these processes would still account for less than half of the organic carbon supply. Considering the paucity of data on processes such as atmospheric deposition, and the interannual variability in processes such as runoff, the significance of the above sources cannot be ruled out with assurance. On the other hand, they must be considered of lower priority in trying to understand the supply of energy to the food web.

Ignoring physical transport for the moment and standardizing on the basis of unit area, South, Central, and San Pablo bays have similar annual carbon supplies -- 3×10^2 g C m^{-2} yr^{-1} for South Bay, and 2×10^3 g C m^{-2} yr^{-1} for both Central and San Pablo bays. If we estimate "available" carbon loading from Delta discharge into Suisun Bay on the basis of BOD (Sec. A.3.1), then Suisun Bay also has a carbon supply of 3×10^2 g C m^{-2} yr^{-1}. These values are within the surprisingly small range of 150-400 g C m^2 yr^{-1} characteristic of temperate North American estuaries (Nixon 1981a). Except for Suisun Bay, almost all of the known carbon supplies -- that is, not accounting for physical transport -- are currently autochthonous.

We now turn to a consideration of each subembayment, in an effort to further understand the mixture of organic carbon sources in 1980 and the effects of year-to-year fluctuations on this mixture.

A.5.2 South Bay

Conditions in 1980. The dominant energy source for the South Bay food web in 1980 appears to have been phytoplankton productivity (Table A.4). Benthic microalgal productivity could also have been a major source, although the uncertainties inherent in both estimates preclude a more quantitative or more certain conclusion. Tidal marsh export, even allowing for studies that suggest export fluxes can be a factor of three higher, and even assuming a high

availability, was probably small compared to autochthonous productivity. The role of circulation and mixing as a direct organic carbon source is unknown, although physical transport probably acts as a net sink for South Bay POC (Sec. A.4.1). The remaining known sources were almost definitely unimportant, even within their respective ranges of uncertainty.

Interannual variability. Net photic zone productivity P_{np} has been estimated for the channel of South Bay for the period 1980-1987 (Cloern 1990; Fig. A.4). There was no apparent trend in annual production. Although peak productivity varied markedly from one year to the next, the fluctuations in annual production were small. The coefficients of variation (CV) during this period were 26% for annual mean P_{np} and 28% for annual mean volumetric biomass b. The maximum (in 1983) was only about twice the minimum (in 1987) for both productivity and biomass.

A comparison of NWI habitat maps for 1958 and 1985 show a decrease of only about 1% in mudflat area and 10% in tidal marsh area during that period. No evidence, therefore, exists to suggest recent significant trends in either benthic microalgal productivity or tidal marsh export of organic carbon. The absence of long time series for benthic microalgae productivity or tidal marsh export, however, precludes a convincing assessment of interannual changes. Major decreases in tidal marsh did take place between 1850 and 1958 (Atwater et al. 1979), and tidal marsh export could have been a dominant organic carbon source in the nineteenth and early twentieth century.

Point source discharge is the only source with a detailed record for the years prior to 1980. The decrease has been quite remarkable (Fig. A.5), particularly since 1972 when the Federal Clean Water Act required a minimum of secondary treatment for all dischargers. The peak load in 1965 was almost exactly 10 times the 1985 load; the corresponding "available" TOC was probably about 0.3×10^{11} g C, the same as the 1980 estimate for benthic microalgal production. In view of the interannual variability in phytoplankton productivity, municipal wastewater could have been one of the dominant organic carbon sources for the South Bay during the 1960s and early 1970s, at least for years when microalgal activity was low. It is clear from Table A.4 and Fig. A.5, however, that point source discharge no longer plays a large role in the organic carbon supply for South Bay as a whole.

For certain regions contained within South Bay, the role of wastewater, both past and present, may be more notable. The area south of the Dumbarton bridge, for example, experienced an even larger decrease in BOD loading -- about 15-fold between 1960 and 1985 -- than the South Bay as a whole (CRWQCB-SFBR 1987). Sewage loading per unit area was 2.6 times higher in this region in 1985, and both the current role of point sources, as well as the consequences of the decrease since 1960, are probably more important. Separate estimates for phytoplankton productivity and other processes in this zone are not available, however, for comparison.

Mechanisms of interannual variability. Assuming that the South Bay food web is now driven primarily by energy from phytoplankton and, perhaps, benthic microalgae, the controls
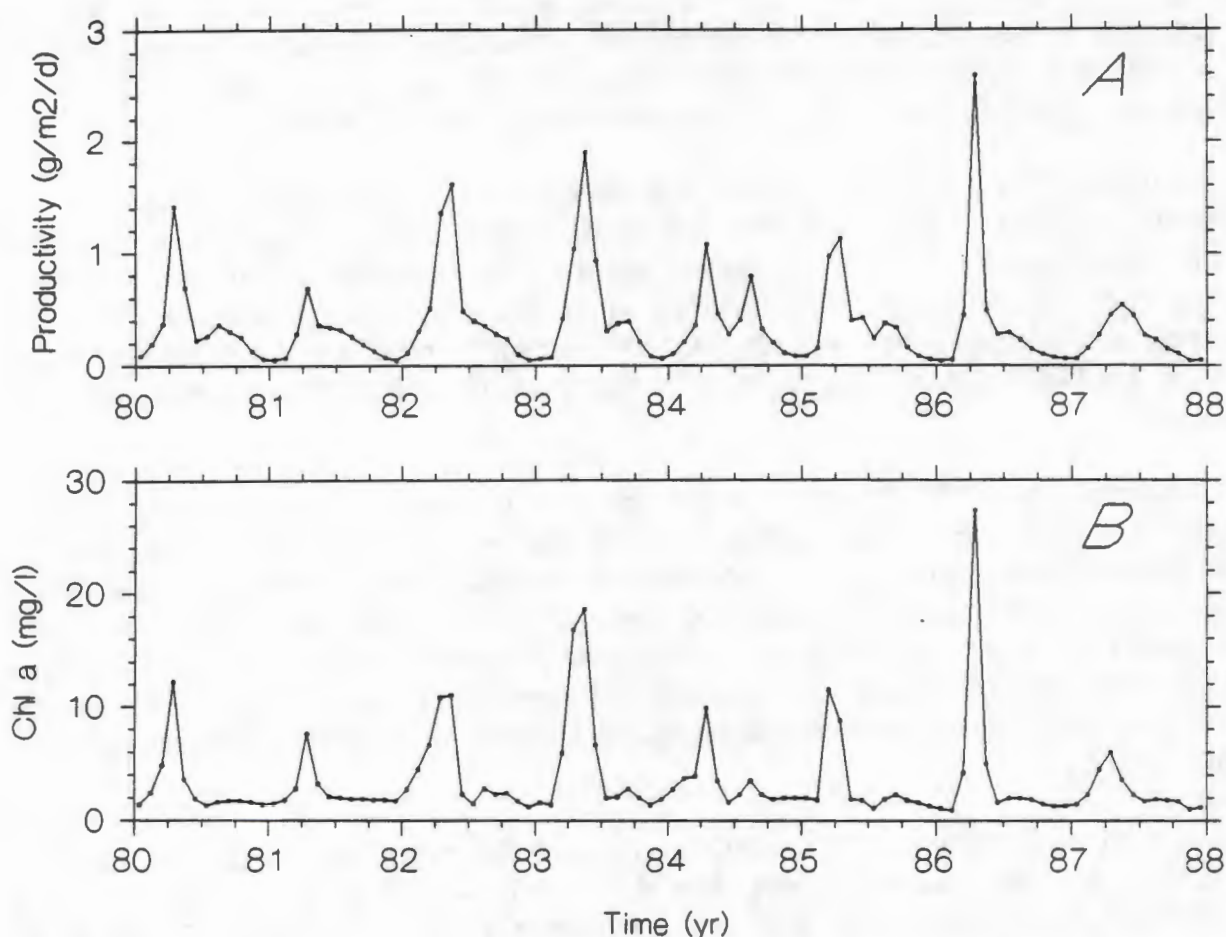
Figure A.4 Monthly mean values for (*A*) photic zone productivity and (*B*) biomass in the channel of South Bay between USGS stations 24 and 30 (data from USGS).

on year-to-year fluctuations in primary productivity are of great interest. Nutrient concentrations typically exceed levels that limit phytoplankton growth rates and are thus not a factor (Conomos et al. 1979). In the absence of nutrient limitation, both net water column productivity P_{nw} (mg C m^{-2} d^{-1}), as well as net photic zone productivity P_{np}, can be shown to depend on three quantities, aside from intrinsic physiological variables: surface irradiance I_0 (E m^{-2} d^{-1}), the ratio of photic to mixing depth Z_p/Z_m, and areal phytoplankton biomass B (mg m^{-2} Chl *a*). This empirical result is true of San Francisco Bay and many other estuaries (Cole and Cloern 1984; Cole and Cloern 1987; Cloern 1987). Assuming a well-mixed water column, it also can be derived from simple theoretical considerations, similar to those discussed by Platt (1986). Understanding variability in P_{nw} is equivalent, then, to understanding what controls surface irradiance I_0, the depth ratio Z_p/Z_m, and biomass B.

Cloern (1979, 1982, 1984) and Cloern et al. (1985) hypothesized a mechanism contributing to interannual variability in South Bay that acts through the depth ratio and biomass.

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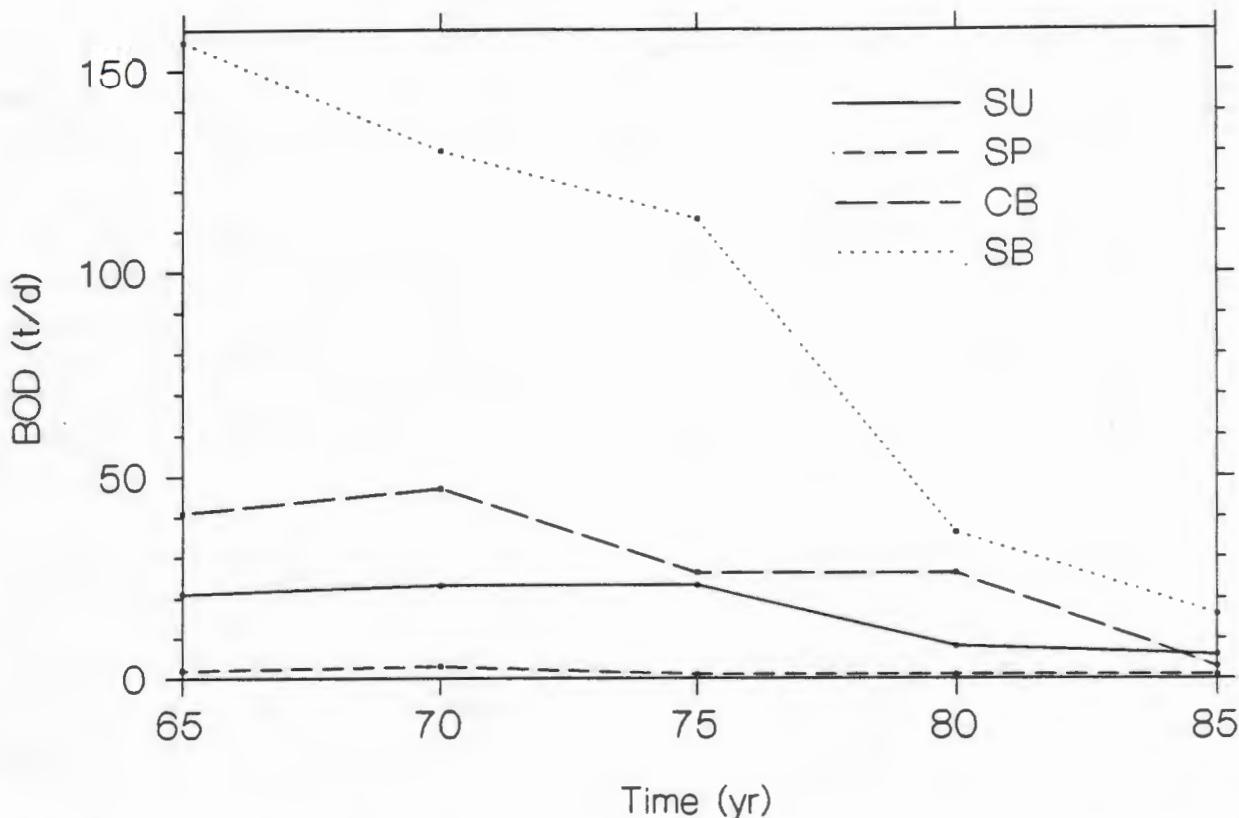
Figure A.5 Five-day BOD loading from municipal wastewater for the major subembayments of San Francisco Bay (data from CRWQCB-SFBR [1987]).

Specifically, when periods of high Delta discharge in winter-spring coincide with periods of low tidal current speed during the tidal cycle, South Bay waters stratify. Apparently, the buoyancy flux from freshwater inflow dominates the dissipation of kinetic energy by tidal mixing at these times. The mixed layer Z_m becomes smaller, which alone would increase the depth ratio. In addition, however, heavier suspended particles sink out of the stable surface layer and turbidity decreases, resulting in a deeper photic depth Z_p and an even larger increase in the depth ratio. The result is an increase in the doubling rate in the mixed layer. Phytoplankton in the mixed layer also become effectively isolated from benthic mollusks, polychaetes, and other suspension feeders, which are capable of filtering the entire water column daily. Phytoplankton biomass is thus released from the constraints of a severe loss process. Although mixed-layer productivity is offset during stratification by respiratory losses below Z_m, it can be shown that the mixed-layer gains will dominate very quickly. The combination of higher Z_p, lower Z_m, and a reduced grazing drain on B thus leads to rapid accumulations of biomass and much higher productivity.

If this mechanism were indeed an important source of interannual variability, we would expect to see a relationship between annual phytoplankton productivity in South Bay and some relevant aspect of Delta discharge. Cloern (1990) provided some evidence along these lines,

using estimates of net photic zone productivity in the channel for the period 1980-1987. Specifically, estimated February-May productivity in the photic zone was correlated with January-April river flow ($p < 0.025$). The statistical evidence, combined with the plausible mechanism outlined previously, supports the hypothesis that river discharge contributes to interannual variability of phytoplankton productivity in South Bay.

Although freshwater flow appears to play a role, the nature and magnitude of the role bears further study. The linear relationship between discharge and productivity accounted for 65% of the variability; a large proportion of the variability remains unexplained, implying that other factors may have an important influence. In particular, the function of local flows directly into South Bay needs attention (J. Cloern 1990, pers. comm.). These flows are sometimes large, they could influence productivity through the same mechanism as Delta discharge, and they could be confounded with the latter.

The analysis, moreover, was based on net photic zone productivity, not net water column productivity. Biomass is highly correlated with net water column productivity, whether for the entire year ($R^2 = 0.79$, $p < 0.01$) or the February-May period ($R^2 = 0.83$, $p < 0.01$). Consequently, respiratory losses below the photic zone are probably higher when P_{np} is higher, and the variability in net water column productivity is probably lower than net photic zone productivity. It is the former quantity, however, that is of main interest, as it represents the energy available to primary consumers.

Finally, 50% of South Bay is shallower than 2.2 m below MLLW (Table A.1). Over 60% of the annual phytoplankton production takes place in shoal areas, defined here as extending to 2 m below MLLW (Table A.3). The relevance of the productivity time series, which was based on data collected at channel stations, is unknown for these shoals. Certainly, the responses of South Bay shoal and channel habitat to mixing forces are different (Powell et al. 1989). Also, the proposed mechanism relating stratification to increased productivity could be inapplicable to shoal areas, which probably do not stratify. Both Z_m and access to phytoplankton by benthic herbivores in the shoals may thus remain unaffected by Delta discharge. Suspended particulate matter (and thus Z_p) and B are still free to respond to Delta discharge and other forces (Cloern et al. 1989). However, the dominant mechanisms underlying fluctuations in these variables and the consequences for annual phytoplankton productivity in shoal regions have not been delineated adequately. In addition to Delta-derived intrusions of turbid water, local streams and runoff and resuspension of sediments may play a role in modulating Z_p (Conomos et al. 1979). Resuspension of chlorophyll (Thompson et al. 1981) also may contribute to variability in B. As resuspension probably decreases Z_m and increases B, the net effects on phytoplankton productivity are particularly hard to assess.

The same phenomena that affect phytoplankton productivity in the shoals can be expected to modulate benthic primary productivity, although not necessarily in the same direction. Resuspension, for example, probably decreases both benthic biomass and the light energy incident on the benthos, resulting in depressed benthic microalgal productivity. Although various

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influences such as resuspension can be described qualitatively, their actual significance has not been measured.

Implications for the near future. As previously mentioned, annual mean P_{np} in the channel had a CV of 26% for the period 1980-1987. If P_{nw} were considered instead of P_{np}, and the variability of shoal areas was included, the apparent year-to-year fluctuations in primary productivity of South Bay could be even less. In contrast, annual Delta outflow (DAYFLOW method) during this period had a CV of 81%, with a maximum more than 13 times the minimum. Thus, even if Delta discharge does underly interannual variability of primary production in South Bay, the effects of river outflow are heavily damped. Annual production appears to be relatively stable.

The recent appearance of the Asian corbulid clam *Potamocorbula amurensis* (Carltōn 1990) introduces a new element of uncertainty, particularly for South Bay south of the Dumbarton Bridge. *Potamocorbula* is currently present, but not abundant, in South Bay both north and south of the Bridge (Carleton 1990). According to a synoptic survey in 1973 (Nichols 1979; Thompson and Nichols 1981), benthic invertebrate biomass south of the Bridge was 50% less than biomass north of the Bridge in summer, 80% less in winter. Organic carbon sources have not yet been tallied for the lower South Bay independently. Little reason exists, however, for expecting a lower food supply, particularly as tidal marsh export, point source discharge, and runoff are probably much higher here than for South Bay as a whole. A potential may be present for higher benthic biomass, increased grazing pressure, lower phytoplankton biomass, and reduced phytoplankton productivity. *Potamocorbula* perhaps can exploit this opportunity because of its apparent ability to withstand a much wider range of sediment types and salinity than other benthic macroinvertebrates (Carleton 1990). In South Bay north of the Dumbarton Bridge, on the other hand, benthic biomass is more typical of intertidal communities (e.g., Knox 1986b). *Potamocorbula* may very well displace certain members of the current estuarine invertebrate community, but the total biomass and consequent grazing pressure may not change dramatically. Note that interannual variability is high among the benthos, despite the absence of long-term trends (Nichols and Thompson 1985b); thus, the applicability of the 1973 data to subsequent years is actually unknown and the suggestions made here highly speculative.

A.5.3 Central Bay

Boundaries for the central basin. Central Bay has often been partitioned into a southern portion, which is regarded as part of "South Bay," and a northern portion, which is regarded as part of "North Bay." Topographic considerations, however, suggest that the central portion should be considered separately, as evidenced by the hypsographs of Fig. A.2. The most informative boundaries for "Central Bay" are not necessarily those delineated by the AHI segmentation scheme. In particular, the region between the San Bruno shoal and the Bay Bridge may have less affinities with the rest of South Bay than with what we have been calling Central Bay (cf. Powell et al. 1986). This point is illuminated further by examining the few relevant time series that exist. From late 1977 through 1980, chlorophyll *a* was measured almost monthly
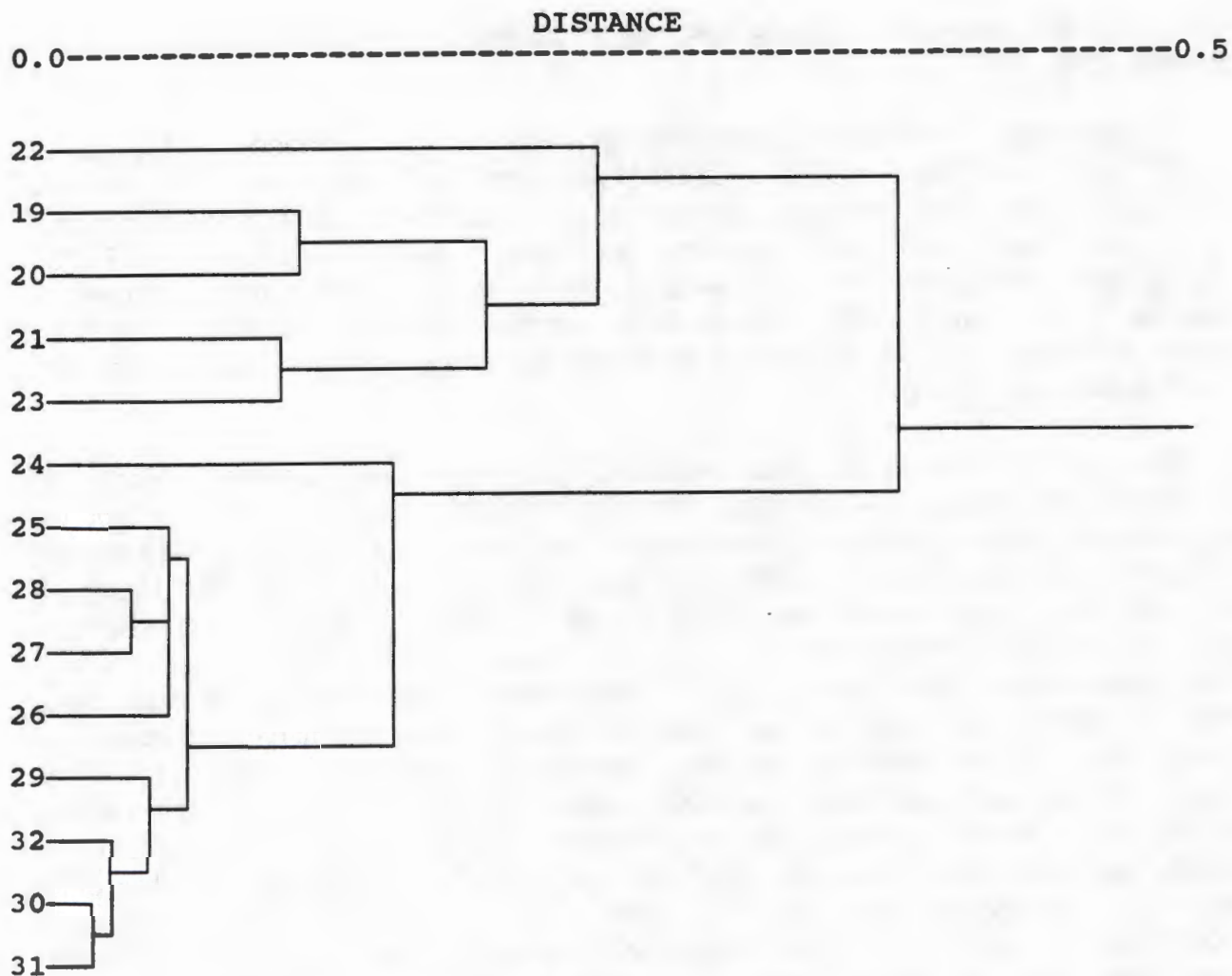
Figure A.6 Tree diagram for Central and South Bay USGS stations 19-32, based on monthly mean chlorophyll *a* for Nov 1977-Dec 1980 (data from USGS).

at 14 channel stations from the Golden Gate down through the South Bay (J. Cloern 1990, pers. comm.). A cluster analysis (nearest-neighbor, Pearson metric) based on monthly mean chlorophyll *a* for these stations revealed a tight grouping south of the San Bruno shoal (USGS station 24) and a second affiliation of stations from north of the shoal to the Golden Gate (Fig. A.6). The northern group of stations was more loosely clustered, indicating higher spatial heterogeneity. The San Bruno shoal itself was a transition region, but it had higher affinity with the tight cluster to the south. This southern group could be further subdivided by the San Mateo Bridge (USGS station 29) into a "tight" southern cluster and a "looser" northern cluster. The results of the cluster analysis are quite consistent with studies of zooplankton distribution (Ambler et al. 1985) and mesoscale chlorophyll variability (Powell et al. 1986). Unfortunately, because of the way the Bay has been subdivided for reporting past studies, it was not possible here to delineate carbon sources within these perhaps more meaningful boundaries.

Conditions in 1980. Central Bay -- as defined by the AHI segmentation scheme -- was dominated by phytoplankton and benthic microalgal productivity in 1980, at least as far as the "known" carbon sources were concerned (Table A.4). Point sources and dredging contributed significant amounts, but were almost definitely of secondary importance.

The flux of organic carbon from both South and San Pablo bays is unknown and could very well have been a significant source. The longitudinal profile of annual mean chlorophyll *a* in 1980 suggests transport of chlorophyll into Central Bay from San Pablo Bay and from South Bay, at least from south of the San Bruno shoal (Cloern 1987, Fig. 4). As discussed previously, the winter gradient of surface POC also suggests transport into Central Bay from both adjoining subembayments, but the summer gradient is less certain (Conomos et al. 1979).

The coastal ocean also may have functioned as a net source of chlorophyll and possibly POC. In 1980, the annual mean extinction coefficient decreased toward the Golden Gate and, as a result, estimated annual productivity reached a Central Bay maximum at this boundary with the coastal ocean (Cloern 1987). It is thus possible that the lower extinction coefficient and, perhaps, decreased benthic grazing pressure compensated for the higher mixing depth. Annual net productivity may have actually been higher just outside the Golden Gate. If higher productivity were reflected in higher biomass accumulations, then the net chlorophyll flux could very well have been into the Bay. On an annual basis, the mean chlorophyll gradient is uninformative, however; the gradient within Central Bay is very weak, from the boundary with San Pablo Bay down to the San Bruno shoal.

Interannual variability. Whatever the exact boundaries that best further understanding, the central basin has been relatively overlooked both in long-term biological sampling and in delineation of causal mechanisms. In particular, no long-term chlorophyll series exist to adequately characterize interannual variability of either phytoplankton or benthic microalgae.

As in South Bay, wastewater discharge must have been a significant source of organic carbon in the recent past. Peak values occurring in 1970 (Fig. A.5) were equivalent to 0.1×10^{11} g yr^{-1} of "available" TOC. This value is comparable to both estimated phytoplankton and benthic microalgal productivity, especially when we recall that the latter two processes have uncertainty ranges of at least 50% (Table A.4). Point source discharges no longer appear to play an important role in the carbon budget of Central Bay.

Transport associated with dredging exhibits high interannual variability (AHI and PWA 1990). The quantity moved from South Bay to the Alcatraz site in 1987, for example, was about twice the 1986 amount. Because dredging transport appears to be a secondary source of organic material, the interannual variability probably has little direct effect on the supply of organic carbon to the Central Bay food web. In the absence, however, of long-term data for the dominant processes -- phytoplankton and benthic microalgal productivity -- a role for dredging during certain years cannot be ruled out with assurance.
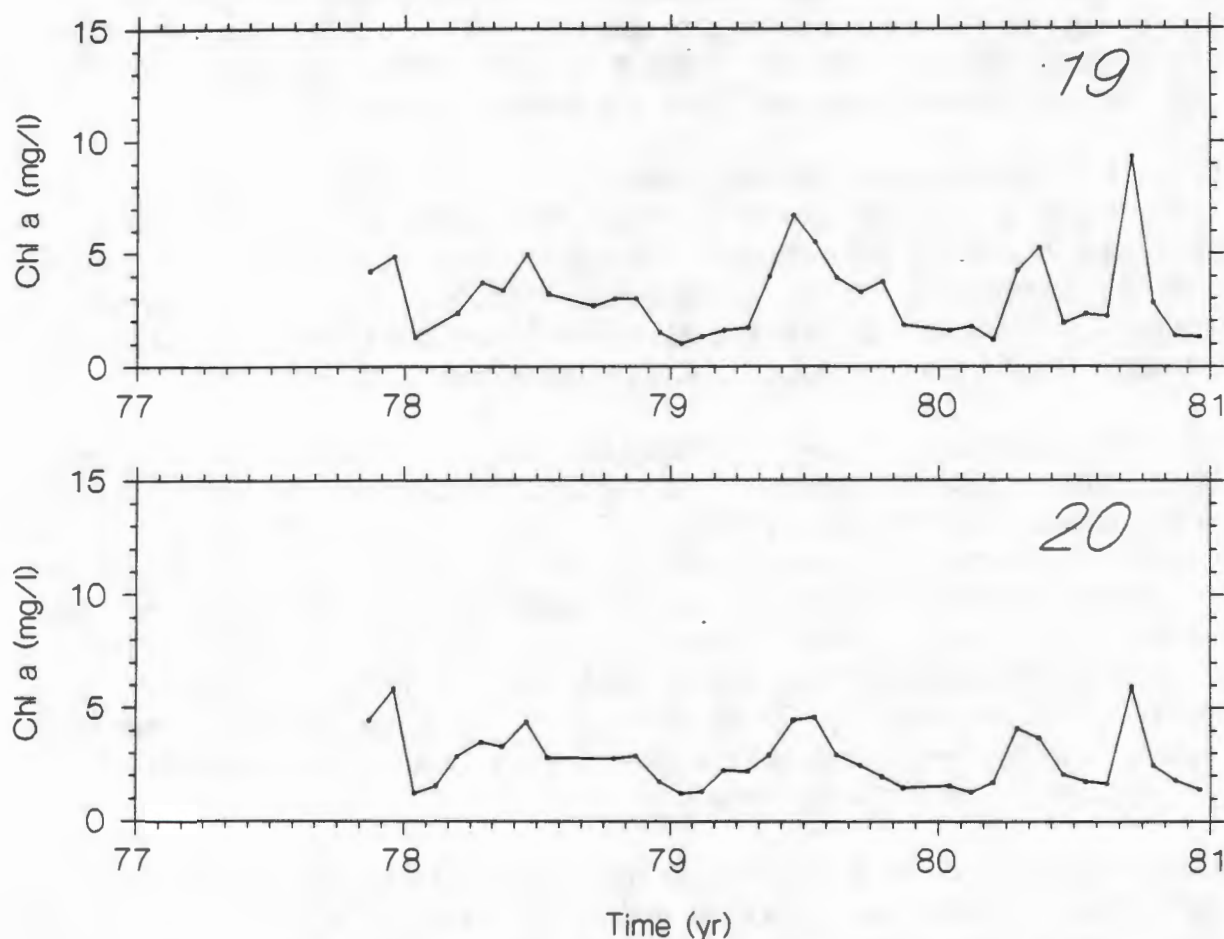
Figure A.7 Monthly mean chlorophyll *a* at Central Bay USGS stations 19 and 20 (data from USGS).

Mechanisms of interannual variability. Based on the cluster analysis described above and the likelihood of imports from adjoining subembayments and the coastal ocean, one would expect the mechanisms to be very different from South Bay proper. The 1977-1980 data for central basin USGS stations 19 and 20 allow a finer appreciation of this point (Fig. A.7). A chlorophyll pulse occurred in December 1977, for example, dominated by *Nitzschia seriata*, a neritic diatom, which suggests an influx through the Golden Gate of a coastal bloom (Cloern 1979). Major biomass peaks for 1978-1980 occurred in May-June and sometimes in September-October at these stations. In contrast, South Bay stations have earlier biomass peaks slightly lagging Delta discharge (Cloern 1990); in 1980, for example, South Bay chlorophyll attained a single maximum in early April (Cloern et al. 1985). Although San Pablo Bay exhibits biomass peaks during May-June as well, the fall peak in Central Bay appears to be disconnected from the adjacent subembayments (Ambler et al. 1985, Fig. 2D). This difference in seasonal patterns between embayments suggest that the nature and causes of interannual variability differ as well. Unfortunately, the available data allow only inconclusive speculation, in the case of both phytoplankton and benthic microalgal productivity.

A.5.4 San Pablo Bay

Conditions in 1980. Phytoplankton productivity was also probably the dominant energy source for the San Pablo Bay food web in 1980 (Table A.4). Benthic microalgal productivity could have been a significant secondary source, but appears to have been relatively less important than in South or Central bays. Tidal marsh export was estimated to be the same magnitude as benthic primary productivity, but was relatively more important than in South and Central bays. Point sources were unimportant. As usual, the amount of organic carbon transferred from other subembayments was unknown but possibly significant.

Interannual variability. As in Central Bay, interannual variability of phytoplankton activity is difficult to characterize and to understand because of the paucity of long-term chlorophyll or productivity measurements in San Pablo Bay. During 1971-1973, chlorophyll samples were collected from both shoal and channel sites, but routine sampling has since been confined to channel sites near the Pinole shoal area (D42 until 1980, D41 since 1980: Ball 1987a). It is particularly unfortunate that no long-term data series are available for the shoals, as a majority of annual phytoplankton production probably takes place in the shallower region (Table A.3). Based on the study of seasonality during 1980 (Cloern et al. 1985) and the chlorophyll data that do exist for San Pablo Bay (Ball 1987a), interannual variability of phytoplankton has been attributed to processes similar to those of Suisun Bay. Much more data is available for Suisun Bay, so we defer the discussion of this variability to the following section.

Tidal marsh habitat area for San Pablo Bay may have undergone a larger reduction in recent decades than for South Bay (Atwater et al. 1979). The importance of tidal marsh export in the recent past hence may have been higher than in 1980 or later years. Unfortunately, the NWI habitat data for 1958 have not been digitized for San Pablo or Suisun bays, rendering a comparison with the 1985 data impossible at this time.

Point source discharge has never been important, even in 1970 when it peaked at a BOD load equivalent to 0.01×10^{11} g C yr^{-1} (Fig. A.5).

A.5.5 Suisun Bay

Conditions in 1980. Suisun Bay departs from the other subembayments in terms of organic carbon sources (Table A.4). For the others, phytoplankton productivity was the dominant, or at least a major, known source in 1980, with a possible major role for benthic microalgal productivity in South and Central bays. Benthic microalgal productivity also played a significant role in San Pablo Bay. In contrast, the dominant organic carbon source for Suisun Bay may very well have been Delta discharge; it appears to have dominated even if we consider only 10% to have been available to the food web of Suisun Bay (Sec. A.3.1; but see Sec. A.6). Phytoplankton productivity was of secondary importance. Tidal marsh habitat area may have decreased between 1980 and 1985, the year for which export estimates were made, but even the

data for 1985 implies that tidal marsh export rivalled and perhaps even exceeded phytoplankton productivity. In contrast to the other subembayments, benthic microalgal production appears to have been minor, as do point sources. Physical transport of organic material from San Pablo Bay may be mediated by gravitational circulation, but quantitative estimates of transport do not exist.

Two additional pieces of evidence support the view that phytoplankton productivity is not a dominant organic carbon source for Suisun Bay. First, the stable isotope results of Spiker and Schemel (1979) suggest that most POC in the entrapment zone (see below) may at times be of riverine origin. Second, bacterioplankton productivity at channel stations in Suisun Bay can greatly exceed phytoplankton productivity (J.T. Hollibaugh and P.S. Wong, pers. comm. 1991), suggesting that significant alternative sources of labile organic matter are present in the subembayment.

Of all the subembayments, tidal marsh export appears to have the greatest potential role in Suisun Bay, for several reasons. First, recall that the upper range for TOC export -- not including possible export of reduced sulfur -- is a factor of three higher than the estimated export. Its uncertainty range thus overlaps estimates of pigment-related carbon, POC, and "available" TOC loading from river flow in 1980 (Sec. A.3.1). Second, the morphometric characteristics of Suisun Bay tidal marsh may facilitate tidal exchange of materials with the open water. In particular, based on NWI map data, the ratio of tidal channel to vegetated tidal marsh is only 1% for both South and San Pablo bays, while it exceeds 7% for Suisun Bay. One might expect a correspondingly larger export flux for Suisun Marsh. Finally, operations in the marsh include periodic flushing of duck ponds and their ample organic matter stores, which may enhance marsh export of organic carbon, although the quantitative importance remains unknown.

As discussed previously, the availability of organic carbon exported from tidal marsh is a mystery. The stable isotope work of Spiker and Schemel (1979) is sometimes cited as evidence that tidal marsh export is insignificant in San Francisco Bay. These authors actually claimed merely that "detritus originating from *Spartina* marsh grass...was not identifiable as an important carbon source" in South Bay. This claim is consistent with the results for South Bay summarized in Table A.4, but several points should be noted in regard to the northern reach. First, the data consisted of only four channel transects, three of them during the 1976-1977 drought, and included no sediment samples for the northern reach. Second, the interpretation of single isotope studies with $\delta^{13}C$ is ambiguous for a number of reasons, particularly when several possible isotope sources are present and the sample has intermediate isotopic values (Peterson and Fry 1987). Third, as noted in a previous section, marsh export may be in the form of reduced sulfur; autotrophic sulfur bacteria have a range of $\delta^{13}C$ values encompassing riverine, estuarine, and most marine phytoplankton values (Peterson et al. 1980; Fry and Sherr 1984). Clearly, additional stable isotope studies of San Francisco Bay are necessary if any definitive conclusions regarding marsh export are to emerge from this method.

Interannual variability. Although interannual changes in riverine TOC loading cannot be evaluated, data do exist for an assessment of year-to-year fluctuations in the pigment-related carbon carried by Delta outflow. As discussed previously, carbon associated with chlorophyll
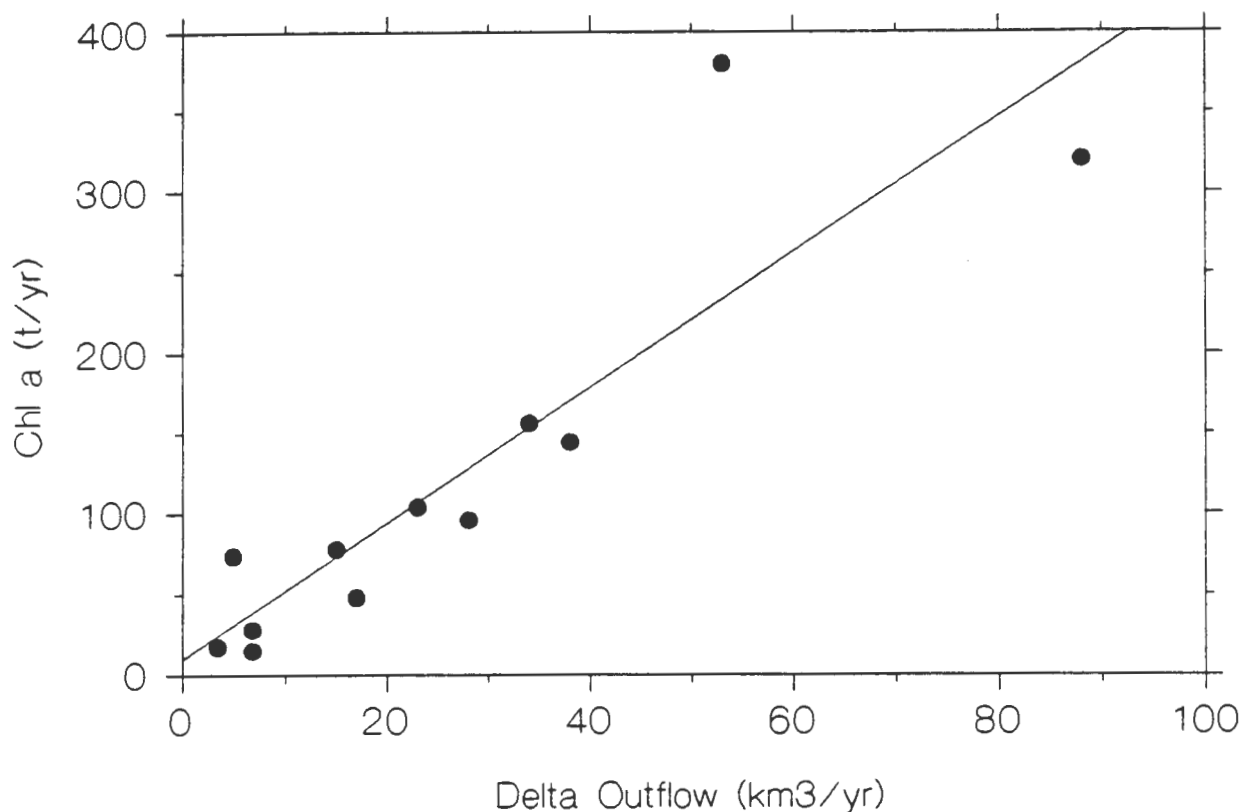
Figure A.8 Chlorophyll *a* loading, based on measurements from surface waters near Pt. Sacramento (D4), from 1976-1987 (data from DWR).

and its degradation products may account for much of the POC loading, and these materials may constitute most of the TOC loading actually available for consumption. Chlorophyll concentrations near the juncture between Suisun Bay and the Sacramento River at Point Sacramento (D4), combined with Delta outflow values, were used to estimate a flow-weighted loading of chlorophyll into Suisun Bay for 1976-1987. Loading of chlorophyll into Suisun Bay was strongly related to flow (Fig. A.8). In other words, the year-to-year fluctuations in riverine loading largely reflect the corresponding variability in Delta outflow. The current drought period that began in 1987, in particular, is probably a time of highly reduced chlorophyll loading from Delta outflow.

Part of the BOD load carried into Suisun Bay can be attributed to upstream point source dischargers (Sec. A.3.1). In the early 1970s, this load amounted to at least 14.4×10^9 g yr^{-1} BOD$_5$, falling off to 3.2×10^9 in 1979 (Hansen 1982). The significance of the decrease during the 1970s is uncertain. The estimates are minimum values and the actual decrease in point source discharge may have been much higher; on the other hand, much of the TOC in discharge may have been respired before reaching Suisun Bay. The BOD$_5$ from the Chipps Island station (D10) is informative, as it covers this time period approximately (Fig. A.9). No trend is apparent in this series, suggesting that upstream changes in municipal wastewater discharge did not affect
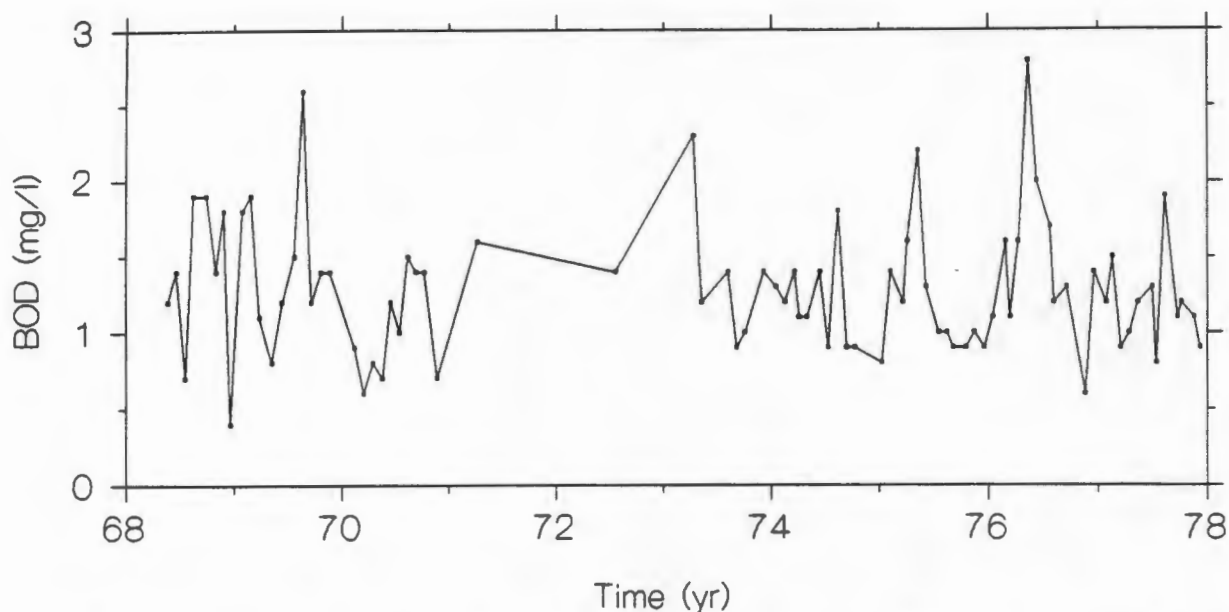
Figure A.9 Five-day BOD values measured in surface waters at a station near Chipps Island (D10; data from DWR).

the TOC loading to Suisun Bay. The evidence is not conclusive, however, as the Chipps Island station is subject to influences from within Suisun Bay as well as from Delta discharge. Note also that the BOD_5 pool does not necessarily reflect the rate of BOD_5 loading. Unfortunately, long BOD series from upstream sites do not exist.

Primary productivity measurements in Suisun Bay were repeated during 1988, a "very dry" year (Delta discharge of 4.7 km^3), permitting a fruitful comparison with the data of 1980, an "intermediate" year (A. Alpine and J. Cloern 1990, pers. comm.). Productivity during 1988 was much lower than in 1980; net annual photic zone productivity π_{np} fell by a factor of five at shoal and channel stations. The drop in π_{nw}, which is simply π_{np} corrected for aphotic respiration (Sec. A.2.1) , was probably smaller but nevertheless substantial. This decreased productivity was due to lower phytoplankton biomass, not lower growth rates.

Phytoplankton productivity in Suisun Bay -- even more so than for the other embayments -- is overwhelmingly dominated by shoal productivity (Table A.4). The 1980 data, for example, imply an annual phytoplankton productivity π_{nw} of 5.2 x 10^9 g C yr^{-1} in the shoals, compared to a negative value of -0.48 x 10^9 g C yr^{-1} in the channel (Table A.3). Interannual variability in embayment productivity must therefore reflect fluctuations in shoal, not channel, productivity. The decrease in productivity between 1980 and 1988 was largely attributable to biomass changes, and not to a change in photic depth (which actually increased in 1988) or insolation (A. Alpine and J. Cloern 1990, pers. comm.). If biomass is generally the controlling factor for productivity in Suisun Bay, it follows that shoal biomass fluctuations should be a guide to variability in embayment productivity. In particular, the long-term data for chlorophyll *a* at a Grizzly Bay

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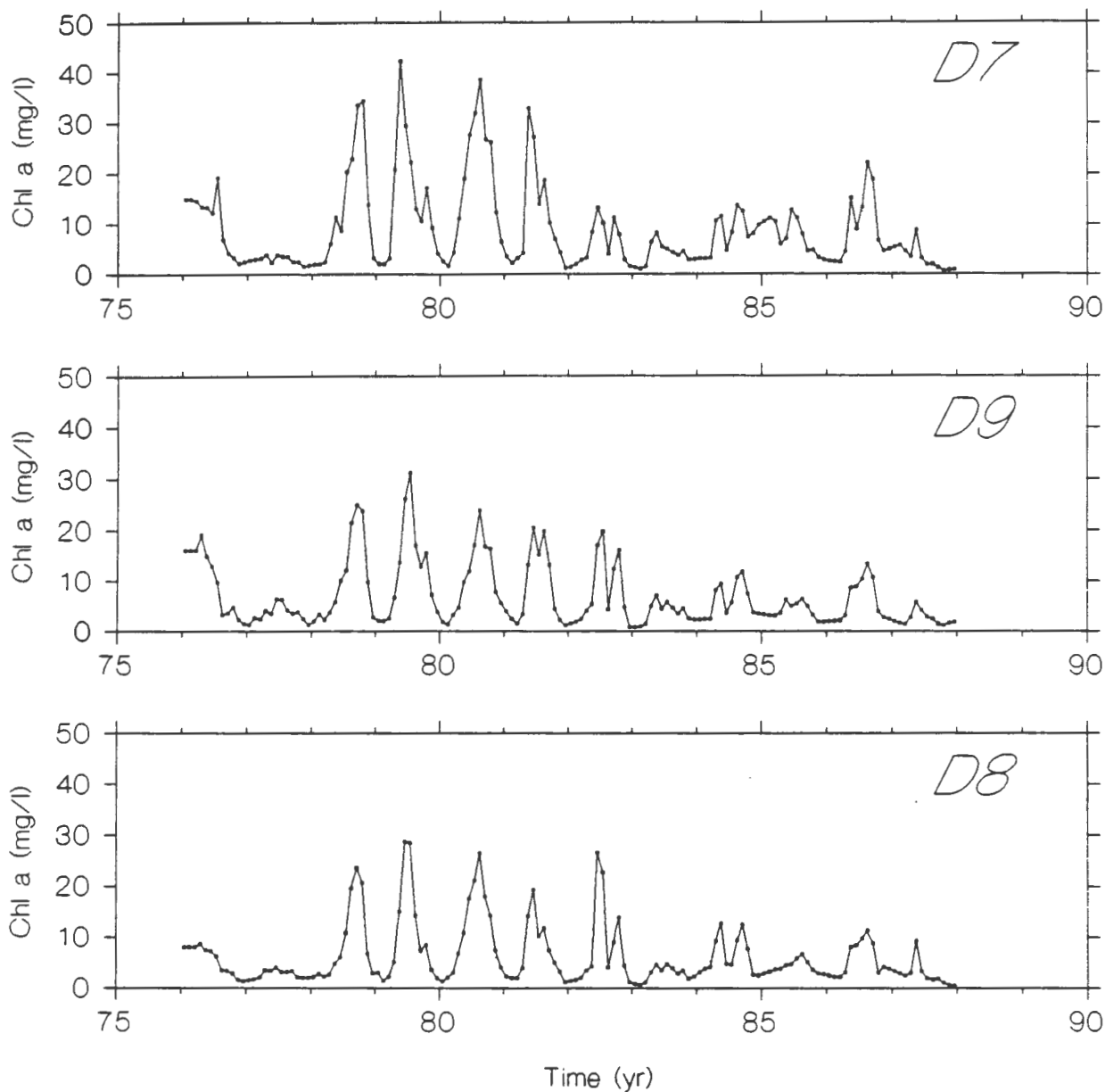
Figure A.10 Monthly mean chlorophyll *a* concentrations in Grizzly (D7) and Honker (D9) bays, and in the channel of Suisun Bay (D8; data from DWR).

(D7) and a Honker Bay (D9) shoal station suggest that phytoplankton productivity in Suisun Bay has been depressed since 1982-1983 (Fig. A.10). Productivity in 1977 also appeared to be low.

As in San Pablo Bay, recent trends for tidal marsh area cannot be evaluated. Point sources, when they were four times higher in 1970 (Fig. A.5), may sometimes have been as significant as phytoplankton or tidal marsh sources, but even then they would have been secondary to loading from Delta discharge.

Mechanisms of interannual variability. Loading of organic carbon from Delta discharge depends both on the volume of discharge and the riverine concentrations of phytoplankton and other forms of labile organic materials. The details of phytoplankton dynamics upstream of Suisun Bay are beyond the scope of this analysis. It should be noted, nonetheless, that several long-term changes in upstream chlorophyll concentration and community composition have occurred since 1973 (see Ball 1987a,b for a detailed analysis). Despite these trends and other types of interannual variability in riverine concentrations upstream, annual chlorophyll loading in recent years appears to be largely proportional to annual Delta discharge (Fig. A.8). Variability in river-borne phytoplankton is evidently inadequate to mask the effects of flow volume.

As pointed out previously, the key to understanding phytoplankton productivity in Suisun Bay is a comprehension of the processes controlling shoal phytoplankton biomass. The same can be said for San Pablo Bay, where three-quarters of the 1980 production took place in the shoals (Table A.3). Two main processes underlying interannual variability have been implicated. The first is the effect of Delta outflow on the residence time for phytoplankton biomass. Much of the work on phytoplankton activity within the northern reach of San Francisco Bay has focused on the significance of the entrapment zone resulting from estuarine circulation (Peterson 1975). Net water column productivity is almost always negative in the channel because of the low Z_p/Z_m ratio, so biomass must be imported for accumulation to take place. During periods of high Delta outflow, an entrapment zone becomes positioned in the channel of San Pablo Bay that increases the residence time of algae dispersed from shoals by tidal mixing and allows such biomass accumulation. As flows decrease, the entrapment zone moves into Suisun Bay where it performs a similar function (Sec A.5.5). During particularly low flows, the entrapment zone is located in the western Delta. A second entrapment zone in the vicinity of the Pinole shoal at lower Delta outflows down to about 300 m^3 s^{-1} has been suggested (Williams and Hollibaugh 1987), but this has been disputed (Ball 1987b). Arthur (1975) first hypothesized that positioning of the entrapment zone relative to large expanses of shoal area was the most critical factor regulating accumulation of phytoplankton in the zone. Further work has largely borne out this contention (Arthur and Ball 1979, 1980; Ball 1977, 1979; Cloern et al. 1983, 1985; Catts et al. 1985; Ball 1987a).

Although the position of the entrapment zone clearly affects the spatial distribution of chlorophyll and POC, the spatial distribution of primary productivity need not reflect that of biomass. When an entrapment zone is present, the residence time for certain phytoplankton taxa and detrital particles is increased and physical transport losses are thus smaller. Perhaps even more important, the concentration of food particles permits more efficient feeding by the planktivores known to frequent the zone. Nonetheless, in the channel, the zone may still be an area of reduced or even negative primary productivity because of a low Z_p/Z_m ratio. If productivity is negative in a region, then biomass accumulation only enhances respiratory losses. For the entrapment zone to stimulate primary productivity, shoal residence time must be effectively increased by its proximity. This is probably, in fact, the case: By decreasing the gradient of biomass between shoal and channel, the entrapment zone probably suppresses net mixing losses of biomass from the shoals. Indeed, the close relationship between shoal and

channel chlorophyll testifies to the effectiveness of tidal mixing between the two regions (Fig. A.10).

The relationship between the entrapment zone and shoal biomass (and, presumably, productivity) is not a simple one. Rather than determining a unique biomass, the location of the entrapment zone appears to set bounds on a range of possible biomass levels. This can be most easily appreciated by examining the relationship between chlorophyll and Delta outflow at a shoal station (D7; Fig. A.11). River flow creates an envelope of possible chlorophyll concentrations that narrows at both high and low flows. The maximum of the smoothed scatterplot (LOWESS algorithm: Cleveland 1981) occurs at about 250 $m^3 s^{-1}$, the approximate center of the flow range that positions the entrapment zone in Suisun Bay. But chlorophyll values are quite variable within the envelope and it is clear that positioning of the entrapment zone is not the whole story.

An additional source of interannual variability in biomass appears to be consumption by benthic herbivores. Nichols (1985) detailed how the Atlantic soft-shell clam *Mya arenaria* and other estuarine benthic invertebrates become established in Suisun Bay during drought periods such as 1976-1977. The larvae are carried upstream in the river-induced gravitational circulation and are able to colonize sites in Suisun Bay when salinity increases during dry years. In 1977, the estuarine species achieved densities sufficient to filter the entire water column approximately once per day. Similar appearances of *Mya* in 1962, 1981, and 1985 in Grizzly Bay suggest that about 16 months of consecutive low river inflow were necessary for successful colonization to take place (Nichols 1990). The return of higher inflows eliminates estuarine species, resulting in decreased feeding pressure from the benthic invertebrate community.

This relationship between prolonged low river flow and temporary invasion by estuarine benthic invertebrates may have been upset in 1987 by the appearance of the Asian corbulid clam *Potamocorbula amurensis* (Carlton 1990). The clam was probably introduced from the western Pacific by the release of seawater ballast into San Francisco Bay in the mid-1980s. By 1987, *Potamocorbula* had become numerically dominant at shoal and channel sites in both Suisun and San Pablo bays, and was also present at some South Bay sites. The rapid spread has been attributed to a depauperate benthic community following the flood in early 1986, which resulted in a lack of competition from pre-existing species (Nichols 1990). Low river inflow had again become prolonged for a period of 16 months by 1988, but *Mya arenaria* did not appear in its usual numbers, apparently excluded somehow by the new arrival.

Implications for the near future. Low phytoplankton productivity may persist as long as conditions -- namely low freshwater flows -- favor estuarine benthic macroinvertebrates. Although riverine loading probably will increase once flows are restored, the same cannot be said of phytoplankton productivity. *Potamocorbula amurensis* is able to tolerate an extremely wide range of salinity (at least 1-30 $^o/oo$), suggesting that it will not be dislodged by the return of higher river inflows (Nichols 1990). If so, enhanced grazing pressure from benthic invertebrates will continue, depressing local populations of phytoplankton and perhaps benthic microalgae. Lower microalgal productivity could therefore persist for some time.
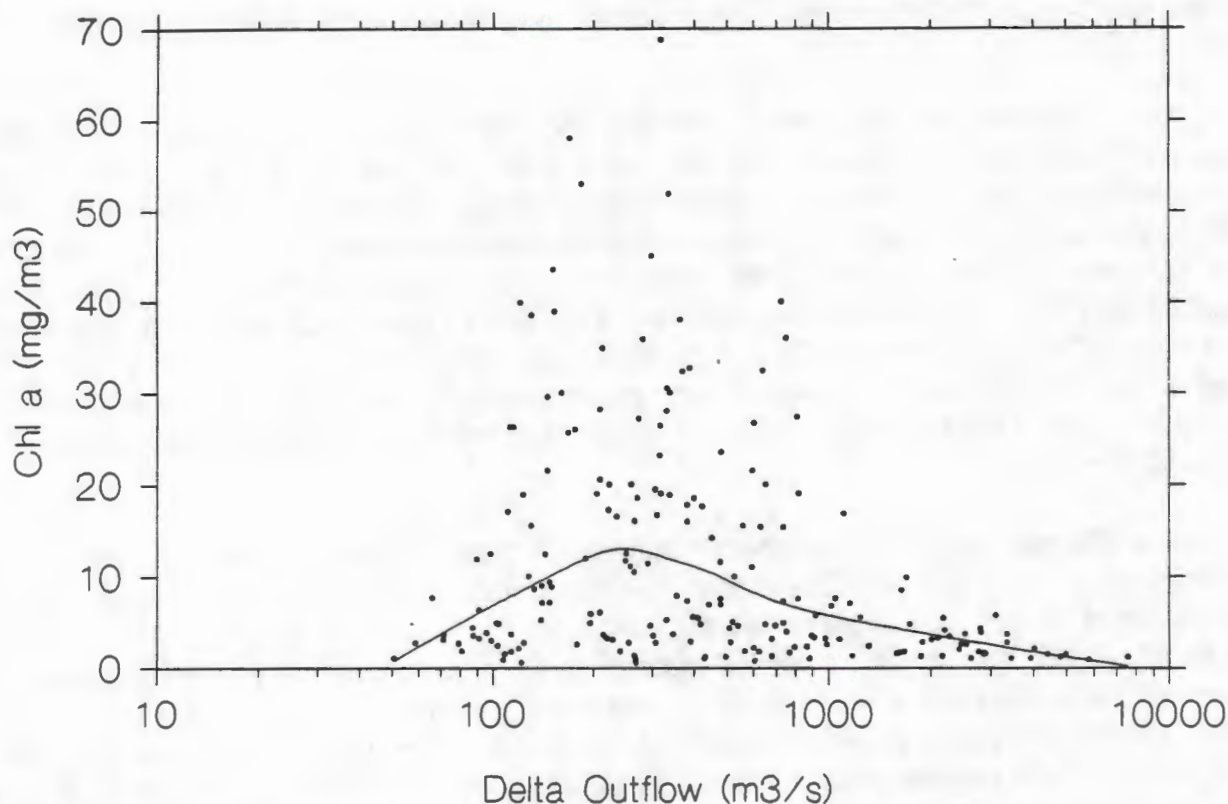
Figure A.11 Monthly mean chlorophyll *a* vs. Delta outflow in Grizzly Bay shoals (D7), Mar 1971-Sept 1988; *solid line*, LOWESS fit (data from DWR).

As long as Delta discharge is low, organic carbon loading should remain at depressed levels as well. In contrast to microalgal productivity however, riverine organic carbon sources should be restored with the return of higher flows. As a result, the relative importance of organic carbon from riverine loading can only increase. Given the apparent dependence of chlorophyll and perhaps "usable" TOC on annual Delta discharge, the relation between organic carbon sources for the food web and the magnitude of Delta discharge may thus become even more clearcut with the presence of *Potamocorbula*.

The response of marsh export to river discharge is of interest. The magnitude of Delta outflow undoubtedly has some modulating effect on exchange between tidal marsh and open water. The smaller freshwater supply during drought conditions also should favor the spread of estuarine macrophytes in their competition with freshwater macrophytes, changing the habitat areas available for higher organisms. But if the net effects on marsh export are damped compared to the response of organic matter loading and phytoplankton productivity, then marsh export may increase in importance during drought periods. Consider, for example, 1988, when Delta outflow was only 14% of its 1980 value. If "available" TOC loading changed in proportion to Delta outflow, and phytoplankton productivity decreased by a factor of, say, three, then Delta loading and phytoplankton productivity each would have amounted to only 0.02-0.03 x 10^{11} g

C yr-1. In comparison, if tidal marsh exports were unaffected by outflow, estimated export would still be 0.06×10^{11} (Table A.4). Tidal marsh export consequently may be a more notable source of organic carbon during drought periods.

A.6 FOOD WEB CONSIDERATIONS

A.6.1 Partitioning between food web and outflow

Previously, we mentioned that an explicit assessment of organic carbon sinks would not be undertaken. Certain aspects of these sinks must be addressed, however, if we are to properly understand the implications of the sources and their respective magnitudes. New organic carbon resulting from either autochthonous production or allochthonous contributions has essentially two possible fates: It can enter the food web through various means, or it can be exported from the region without being utilized. This mass balance can be expressed ideally as

$$\Sigma J_i = (C/T_c) + (C/T_h),$$

where J_i (g m^{-3} d^{-1}) is the ith carbon source; C (g m^{-3}) is the concentration of unutilized organic carbon within the subembayment; T_c (d) is a "primary consumption" residence time, that is, the time that would be required for all primary consumers to strip the subembayment of new organic carbon, either through assimilation by bacteria, zooplankton, or benthic invertebrates; and T_h (d) is a "hydraulic" residence time for new organic carbon due to flushing. Note that T_h is actually different for DOC and various kinds of POC, due to the possible presence of an entrapment zone, but this complication will not obscure the basic point to be made here. The fraction of organic carbon sources entering the food web is thus

$$f_c = (C/T_c)/[(C/T_c) + (C/T_h)],$$

which reduces to

$$f_c = 1/[1 + (T_c/T_h)].$$

The fraction entering the food web at any time accordingly decreases in a simple fashion with the ratio of primary consumption to hydraulic residence times.

Residence times -- and their ratio -- have a marked seasonality. In 1980, for example, monthly mean Delta discharge during January was about 3000 m^3 s^{-1}. Hydraulic residence times in Suisun Bay at these flows are on the order of 1 d (Smith 1987). On the other hand, monthly mean Delta discharge in August was 110 m^{-3} s^{-1}. The corresponding hydraulic residence time is on the order of 10 d (Smith 1987). For purposes of illustration, consider a benthic invertebrate community that filters the overlying water at a rate of 0.2 d^{-1}, constant throughout the year; T_c is thus 5 d. During January, the corresponding f_c in Suisun Bay would be less than 20%, during August, almost 70%. Typically, however, benthic invertebrate populations attain their highest abundance -- and, presumably, lowest T_c -- between spring and fall (Nichols and Thompson 1985b). T_h and T_c therefore tend to be out of phase, implying even a larger seasonality in f_c.

This seasonality in f_c forces us to confront a fundamental deficiency with assessing organic carbon sources on an annual basis: The individual organic carbon sources also change radically with the seasons. In 1980, for example, 35% of DOC imports from the Delta occurred in January, less than 5% in August. Suisun Bay primary productivity, in contrast, peaked in August and was negligible in January. The actual contribution of an individual source to the food web thus depends on the temporal matching of its flux J and f_c. More formally, although the annual contribution of the *i*th carbon source *to the organic carbon pool* is simply the time integral of J_i, the annual contribution *to the food web* is the time integral of $J_i \cdot f_c$. Because high river flow decreases T_h but apparently increases J_i due to riverine loading (Fig. A.8), there is an inherent mismatch between riverine sources and f_c (although the presence of an entrapment zone at 150-300 $m^3 s^{-1}$ [Ball 1987a] would increase T_h and f_c over the values expected on the basis of flow volume alone). Furthermore, because of the inhibitory effect of river flow on consumer populations, the mismatch could be exacerbated by an increase in T_c during high flow. In contrast, seasonality favors the contribution of primary productivity sources to the food web. A higher proportion of organic carbon derived from primary productivity than from riverine sources is probably consumed on an annual basis. These considerations constitute a strong argument for taking the next step in assessing organic carbon sources, namely, aiming for a higher resolution in time.

Although a large proportion of organic carbon sources for Suisun Bay may never enter the food web of the subembayment, particularly in winter, the same cannot be said for the northern reach as a whole. When we consider the quantity f_c for the entire northern reach of the estuary, a much higher fraction probably enters the food web. The northern reach has hydraulic residence times three-fold higher than for Suisun Bay alone (Walters et al. 1985). Furthermore, benthic invertebrate biomass may be substantially higher -- and T_c lower -- in San Pablo compared to Suisun Bay (Thompson and Nichols 1981). Thus, much of the organic matter for Suisun Bay attributed to Delta discharge may actually be consumed within San Pablo Bay.

Assuming that available riverine TOC is 10% of the total riverine loading (Sec. A.3.1), then the combined contribution of all organic carbon sources is 1.1 x 10^{11} g C yr^{-1} for the northern reach (including Suisun, San Pablo, and half of Central Bay sources). For this northern reach as a whole, phytoplankton productivity is the only major source (50%), while benthic microalgal productivity, Delta discharge, and tidal marsh export may be significant secondary sources (10-20% each). A mean $C:O_2$ molar ratio for benthic respiration in San Francisco Bay appears to be about 1 (Hammond et al. 1985). If respired within the estuary, the carbon sources should thus give rise to an oxygen consumption of 2.9 x 10^{11} g yr^{-1}. In comparison, Peterson (1979) estimated a substrate oxygen consumption of 2.3 x 10^{11} g yr^{-1} for the northern reach, about 20% less than our estimate. Peterson's assessment was based on a mass balance for oxygen using primary productivity and respiration measurements for 1976-1977, estimates of transport across the air-water interface, and an assumption that net dispersive transport of oxygen was zero in the horizontal direction. Production in 1976-1977 was probably lower than in 1980 and secondary carbon sources were ignored, so the method used by Peterson (1979) should yield a higher estimate for 1980. The agreement between the estimates made on the basis of organic carbon sources and by Peterson (1979) is remarkable, and perhaps fortuitous in view

of the many approximations and uncertainties involved. Nonetheless, the agreement offers some support for both estimates and implies that most organic carbon sources for the northern reach enter the food web within the reach.

Similar evidence suggests that most South Bay organic carbon sources are consumed within South Bay. Hydraulic residence times for South Bay are much higher than for the northern embayments; T_h is probably on the order of 10^2 d, even during high river flow. Benthic biomass is probably higher, and T_c lower, than for either San Pablo or Suisun bays (Thompson and Nichols 1981). Finally, benthic gas exchange measurements suggest that most of the primary productivity is consumed within South Bay. Hammond et al. (1985) estimated an annual average of 23 ± 6 (SE) mmol m^{-2} d^{-1} ΣCO_2 in 1980, based on quarterly, in situ measurements of benthic flux at both a shoal and channel site. The June 1980 measurement was close to the only previous estimate of benthic flux -- for August 1976 (Hammond and Fuller 1979). The daily average for 1980 is equivalent to an annual consumption of 0.55×10^{11} g C yr^{-1} for South Bay. In comparison, the organic carbon sources in South Bay for 1980 totalled 1.2×10^{11} g C yr^{-1}. About half of the estimated production thus appears to be metabolized on the bottom. Additional respiratory losses must take place in the water column through bacterial and zooplankton metabolism. Although oxygen consumption measurements have been published for the water column of the northern reach (Peterson 1979, 1987, 1988), no annual averages have been estimated for South Bay. In any case, the data imply that at least half of the organic carbon sources for South Bay enter the food web within the subembayment.

The high proportion of organic carbon sources apparently consumed within the estuary underlines an important point: Organic material which is unavailable to one population because of size, shape, composition, or precise location may have many other opportunities to enter the food web. For example, the alga *Melosira granulata*, common in Suisun Bay and especially parts of the Delta (Herrgesell 1990), is not a particularly good food source for zooplankton because of its hard siliceous frustule. On the other hand, these *Melosira* filaments undoubtedly die within the estuary and become incorporated into the food web through bacterial decomposition or perhaps direct consumption by benthic invertebrates.

Physical transport remains a possible complicating factor in interpretation of the oxygen data. For example, it is possible -- at least logically -- that physical transport results in both significant organic carbon sources and biomass losses. If the two approximately balance, then primary productivity and community respiration could appear to balance as well; it would be erroneous in that case, however, to conclude that respiration was the only significant fate for primary productivity. In fact, for estuaries as a group, annual benthic respiration accounts for an average of only about 25% of organic carbon sources (Nixon 1981b), substantially less than what the data appear to imply for San Francisco Bay.

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A.6.2 Organic carbon sources and higher organisms

The effect of food supply on aquatic resources of the Bay can be broken down into three successive issues: (1) the supply of new organic carbon by primary productivity and imports; (2) the partitioning of this new organic carbon between an unutilized outflow and entry into the food web; (3) and the flow of organic carbon from new organic carbon entering the food web to the populations of interest, whether they be fish, shellfish, and so on. Previous sections have dealt with the first two issues -- particularly the first -- in some detail. The last issue is the most complex one, and certainly the least understood. It is not possible to be as systematic about organic carbon flow *within* the food web as we have tried to be about organic carbon sources *to* the food web. One particular finding based on studies of many estuaries, however, is worthwhile reviewing here.

Despite our lack of knowledge regarding the particulars of food webs, certain simplifications have emerged regarding fish production from a synthesis of work in many different aquatic ecosystems. In particular, whether in marine or freshwater systems, fish yield tends to increase with annual primary productivity and, presumably, other organic carbon sources (e.g., Nixon 1988). For marine (including estuarine) systems, fish yield is proportional to the 1.6th power of primary productivity ($R^2 = 0.84$, $p < 0.05$), suggesting that primary productivity changes are amplified in fish yield changes. The slope of the relationship may be even higher for estuaries (Nixon 1988, Fig. 6). Given that organic carbon sources for certain subembayments such as Suisun Bay (Sec. A.5.4) have decreased during the recent drought period, it is tempting, on the basis of this empirical relationship, to conclude that the overall yield of fish and macroinvertebrates must have decreased as well. Although this may very well be true, a number of caveats are in order.

First, even if this rule-of-thumb connecting fish yield and primary productivity does reflect the effects of food supply, it would be unwise to assume too great a precision. The relationship was established with productivity data ranging over a factor of 20. Over the much smaller range probably characteristic of San Francisco Bay during the last decade, the variance explained by this relationship is much less and other factors are correspondingly more significant.

Second, a more recent analysis of total fish yield in coastal and open ocean waters concluded that carnivorous fish production is controlled by the amount of "new" nitrogen (as opposed to recycled nitrogen) annually incorporated into phytoplankton biomass (Iverson 1990). The relationship between fish yield and total primary production (Nixon 1988) is therefore just a surrogate for the true causal relationship between fish yield and "new" primary production. As little evidence exists that San Francisco Bay -- as opposed to the Delta -- is nitrogen-limited, it is unclear how well this relationship can be applied to the Bay.

Finally, the relationship addresses only overall fish yield. Although overall yield may decrease -- a conclusion which cannot be verified for the Bay because of insufficient data -- the same cannot be said for individual species of interest. Each population will react according to its habitat and food requirements, undoubtedly resulting in a shift in species composition.

Drought conditions in San Francisco Bay, for example, not only depress autochthonous and allochthonous energy sources, but also result in relatively more grazing losses to benthic macroinvertebrates (Sec. A.5.4). Benthic food webs are therefore favored, and a greater *proportion* -- not necessarily a greater amount because of the reduced organic carbon supply -- can pass to demersal fish such as sturgeon (*Acipenser transmontanus*; Nichols 1990). If *Potamocorbula amurensis* persists even after drought conditions cease, the increase in relative importance of benthic pathways may also persist.

A.7 DATA AND INFORMATION GAPS

Phytoplankton productivity. Changes in the array of sampling stations are warranted. Two issues in particular need to be addressed. First, primary productivity in shoal areas dominates that in deeper areas, especially in Suisun Bay (Table A.3), yet most data are collected from channel stations. Second, almost no long-term series of chlorophyll or productivity measurements are available for Central and San Pablo bays. Little is known, consequently, about the entrapment zone when it is pushed out of Suisun Bay by high flows. Third, certain areas in South and Suisun bays appear to be oversampled in space, relatively speaking. In the South Bay, for example, the region between San Bruno shoal and the Dumbarton Bridge exhibits much less spatial variability than the region between the Golden Gate Bridge and San Bruno shoal (Fig. A.6). A similar analysis of data landward of the Carquinez Strait reveals tight clusters of stations, such as from Chipps Island to Point Sacramento.

Time series for the Bay are thus characterized by periods with relatively high frequency data, and regions with relatively high-resolution data, interspersed with long gaps in time and space. The irregularity in sampling hinders the potential value of the data that are collected, particularly for understanding the long-term changes that may now be underway globally. A commitment needs to be made to a group of "index stations" that will be sampled at a regular frequency for at least chlorophyll *a* and extinction coefficient (or, equivalently, photic depth) into the indefinite future. Some of the current effort in the channels should be shifted to shoal sites. Similarly, some of the current efforts in South and Suisun bays should be shifted to Central and San Pablo bays. If this basic, "index station" program is made as simple as possible, its longevity would be more likely. The number of stations and the sampling frequency should therefore be as modest as possible. The abundance and distribution of benthic organisms should be carefully considered in choosing index stations, as the benthos provide a kind of "integrated moving-average" indication of chemical and planktonic conditions.

Actual primary productivity measurements are not necessary, as productivity can be deduced from biomass, turbidity, and light availability (Sec. A.2.1). But given the importance of light availability, a permanent station should be established for measuring surface irradiance. The absence of continuous, reliable, irradiance measurements hinders the interpretation of existing data sets.

Assumptions about aphotic respiration have a large effect on estimated productivity, particularly in Suisun Bay (Table A.3). Yet little direct evidence exists on the magnitude of these respiratory losses. Further experimental work on aphotic respiration in San Francisco Bay would be a definite contribution, particularly work that would improve estimates of net water column productivity P_{nw}.

Benthic microalgal productivity. No measurements have yet been made on benthic microalgal productivity, despite their possible significance, especially in South and Central bays (Table A.4). As discussed previously (Sec. A.2.3), prevailing measurement techniques may be

unreliable. Although suitable methods may not be available for San Francisco Bay, this issue does require more attention. At the very least, sampling of sediment chlorophyll could accompany water column measurements at index stations. The product of sediment chlorophyll and light incident on the sediments could serve as a relative index of benthic productivity. Incident light could be estimated from measurements of surface irradiance and extinction coefficient (photic depth) at the sampling stations.

Delta discharge. Delta discharge may be the largest source of organic matter for Suisun Bay and is probably a significant one for the northern reach as a whole (Table A.4). The load of organic carbon to San Francisco Bay from the Delta needs to be measured on a regular basis. Due attention needs to be given to POC as well as DOC, and to bottom samples as well as near-surface samples. Because of the probable episodic nature of organic carbon loading, sampling must be able to resolve the succession of storms that characterize the winter period. Because of the apparent importance of riverine algae, chlorophyll and derived pigments also should be measured in tandem with organic carbon.

The issue of availability needs to be addressed as well. BOD measurement offers one perspective on this problem. Ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.) need to be continued and extended. Additional approaches also must be sought.

Tidal marsh export. Tidal marsh sources may be of importance for Suisun Bay, particularly during drought periods. Direct estimates of tidal marsh export are virtually impossible, in part because of the difficulty in determining residual flows from tidal exchange. The uncertain availability of exported organic carbon is another obstacle. Hence, indirect methods are required to address this question. The use of multiple stable isotope markers appears to be of value. B.J. Peterson et al. (1985), for example, using ^{13}C, ^{15}N, and ^{34}S, was able to show that benthic macroinvertebrates consumed *Spartina* detritus and plankton in preference to terrestrial plant detritus. A similar study in Suisun Bay may be able to determine at least the qualitative significance of tidal marsh export.

In view of the large export of reduced sulfur encountered for some marshes (Sec. A.3.2; Peterson et al. 1980), a preliminary investigation of sulfide oxidation activity related to tidal marsh exports is warranted.

Circulation and mixing. The system boundaries need to be considered carefully in relation to physical transport. At the minimum, transport through the Golden Gate requires definition and should be the first objective. A carbon budget for the entire Bay would then be feasible.

Further subdivision needs to be done carefully, with due regard to topographical features and the existing data. As implied in the previous discussion (Sec. A.5.3), the segmentation scheme normally used landward of the Golden Gate requires some revision. The boundary between South and Central bays, in particular, perhaps should be shifted to the San Bruno shoal. The northern extent of "Central Bay", currently at Point San Pedro-Point San Pablo, also

requires re-examination from a hydrodynamic point of view. In addition, the utility of the boundary between San Pablo and Suisun bays needs to be addressed. The entrapment zone, as well as organic matter from riverine loading, moves freely across the boundary as flows increase. From the point of view of establishing subregions for a carbon budget and subsequent food web analysis, the distinction between the two subembayments may have little value. On the other hand, a further subdivision of South Bay at the Dumbarton Bridge appears warranted, in view of the higher point source loading, relative tidal marsh area, and runoff south of the bridge. A lack of primary productivity measurements in lower South Bay would be an impediment to this subdivision, something to be considered also in the choice of index stations (see above).

Whatever the boundaries, direct measurements of transport are an unrealistic goal, for the same reason that tidal marsh export cannot be assessed with any accuracy. But the flow field can be characterized from existing data and modeling studies. In principle, the flow data can be combined with concentration data for various organic matter fractions to estimate transport across the major boundaries. In practice, the concentration data does not appear to be adequate in many locations. Modelling studies, therefore, must be accompanied by a supplemental field measurement program for organic matter fractions, particularly DOC, various size fractions of POC, and chlorophyll. At the minimum, measurements are needed at the Golden Gate, including horizontal gradients through the Gate and vertical profiles both seaward and landward of the Gate.

Food web structure. The structure of the food web connecting organic carbon sources to higher organisms is critical in determining the magnitude of their food supply. The number of trophic linkages, for example, is especially important in controlling the efficiency of energy transfer from sources to macroscopic consumers: If energy is transferred with an average efficiency of, say, 10% along each link, then the interposition of an intermediary organism has the same effect as a ten-fold drop in the food supply at the base of the food web.

At the macroscopic level, food webs have been delineated in a number of ecosystems, as recently reviewed by Schoener (1989). At the microscopic level, on the other hand, the relative importance of many postulated pathways has not yet been demonstrated (Mann 1988), for the Bay or for other ecosystems. In view of the nature and number of these microscopic interactions -- involving autotrophs, DOC, bacteria, protozoans and small metazoans -- a complete characterization of the Bay's food web appears to be an unrealistic goal for the near future.

It is possible, nevertheless, that a complete characterization is unnecessary. Circumstantial evidence from other ecosystems suggests that the major pathways through the food web are sometimes relatively simple. Demersal fish production, for example, often has a high efficiency when compared to organic carbon sources for the benthos (reviewed by Mann 1982). Energetic considerations require that settling organic matter be consumed directly by macrofauna and passed to demersal fish in order to account for this high efficiency. If the other components of the benthos do, indeed, have a secondary role, then the current lack of quantitative knowledge regarding bacteria, microfauna, and meiofauna in San Francisco Bay sediments (Nichols and Pamatmat 1988) may not be a major impediment. Note, however, that the "small food web"

consisting of micro- and meiofauna does compete for food with the macrobenthos of some estuaries (e.g., Wadden Sea; Kuipers et al. 1981).

A comparison of benthic macroinvertebrate productivity (e.g., Nichols 1978) with primary productivity would be especially pertinent, particularly during bloom periods when most of the annual phytoplankton production takes place. If macroinvertebrate productivity were a high enough percentage of microalgal productivity, then a direct link from primary producers to the large benthic invertebrates would be implicated. Lower percentages would imply either that intermediate consumers were present in the water column or sediments, or that the planktonic food web was a significant sink for organic matter. A related study in the South Bay is currently in the initial planning stages (J. Thompson 1990, pers. comm.). A similar investigation is warranted for Suisun Bay. The results of these studies, combined with ongoing studies of multiple stable isotope and lipid markers (J. Cloern 1990, pers. comm.), should provide a guide for further research within the benthic habitat.

Even though the major pathway *within* the benthic habitat may be simple, organic matter from primary productivity may undergo transformations *before* coming into contact with the benthos. The number of trophic links in the water column may radically affect the food supply to midwater fish and the benthic habitat, whether these links occur on a microscopic -- via the "microbial loop" (Azam et al. 1983) -- or macroscopic level. Indeed, bacterioplankton production and grazing by planktonic bacteriovores appear sometimes to form a significant pathway in the Bay's food web (Hollibaugh and Wong, pers. comm. 1991). A continued investigation into planktonic microbial processes is therefore warranted. The detailed study of mechanism, however, should be accompanied by attempts to determine whether a few simple pathways dominate. As in the case of the benthos, simultaneous measurement of both organic matter sources and production of the larger planktonic invertebrates may provide the necessary clarification. These measurements would be most informative if done in conjunction with those for the benthos.

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Appendix B

Distribution of regularly occurring fish species
at each of the regularly sampled sites of the CDF&G Bay Study

Species abbreviations used in the following tables are:

AMS	American shad	*Alosa sapidissima*
BAT	California bat ray	*Myliobatis californicus*
BAY	bay goby	*Lepidogobius lepidus*
BRN SMO	brown smoothhound	*Mustelus henlei*
BROK	brown rockfish	*Sebastes auriculatus*
CCAT	channel catfish	*Ameirus punctatus*
DAB	speckled sanddab	*Citharichthys stigmaeus*
DS	Delta smelt	*Hypomesus transpacificus*
ENGL	English sole	*Parophrys vetulus*
JACK	jacksmelt	*Atherinopsis californiensis*
KS	chinook (king) salmon	*Oncorhynchus tshawytscha*
LEOP	leopard shark	*Triakis semifasciata*
LFS	longfin smelt	*Spirinchus thaleichthys*
LOGP	bigscale logperch	*Percina macrolepidotus*
MID	plainfin midshipman	*Porichthys notatus*
NAC	northern anchovy	*Engraulis mordax*
PH	Pacific herring	*Clupea harengeus*
SB	striped bass	*Morone saxatilis*
SF	starry flounder	*Platichthys stellatus*
SP	shiner perch	*Cymatogaster aggregata*
ST	Sacramento splittail	*Pogonichthys macrolepidotus*
STAG	staghorn sculpin	*Leptocottus armatus*
TFS	threadfin shad	*Dorosoma petenense*
TOP	topsmelt	*Atherinops affinis*
WALL	walleye surfperch	*Hyperprosopon argenteum*
WCAT	white catfish	*Ictalurus catus*
WCRK	white croaker	*Genyonemus lineatus*
WS	white sturgeon	*Acipenser transmontanus*
YFG	yellowfin goby	*Acanthogobius flavimanus*

Segment SB4
Bay Study Station 101

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	LFS	SP	PH	TOP		19	798 3665
Apr-Jun	NAC	JACK	SP	PH	LFS		20	878 10639
Jul-Sep	NAC	BAT	JACK	MID			12	345 9823
Oct-Dec	NAC	TOP					14	255 2821

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	SP	STAG	BAY	ENGL	LFS	34	1785 2652
Apr-Jun	NAC	WCRK	SP	BAY	STAG	BRN SMO	22	758 991
Jul-Sep	NAC	WCRK	MID	BRN SMO			24	424 1157
Oct-Dec	NAC	SP					21	212 366

Northern anchovy is the most frequently captured species in both nets. Several fish species increase in abundance during the season when anchovy abundance is low but their small increases are masked by the large drop in catch of anchovy.

Pacific herring and shiner perch are regular components in the midwater trawl from January to June. Jacksmelt are regularly caught from April to September in the midwater trawl. Topsmelt and longfin smelt are caught regularly during parts of the rainy season; topsmelt principally from October to March and longfin smelt from January to June. Bat rays and plainfin midshipmen regularly enter the trawls in summer.

In the otter trawl there is a peak in numbers of species and numbers of fish from January to March. White croaker and brown smoothhounds are regularly caught in the warmer months (April - September). In the cooler months, shiner perch are regularly caught from October to June and bay gobies are caught from January to June.

In both nets there is a peak in number of species and in the number of predictable species from January to June and the least predictability from October to December.

Segment SB7
Bay Study Station 107

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	NAC	LFS				16	1239 3189
Apr-Jun	NAC	PH	JACK	SP			17	623 16733
Jul-Sep	NAC	JACK					13	677 8695
Oct-Dec	NAC	TOP	JACK				15	215 4476

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	NAC	STAG	DAB	BAY	LFS	32	1293 1455
Apr-Jun	WCRK	NAC	SP	BAY	STAG	ENGL	22	738 935
Jul-Sep	NAC	WCRK	SP	BAY	MID		18	486 631
Oct-Dec	NAC	WCRK					19	287 317

As with station 101, northern anchovy is a regular feature of the catch in all seasons in both nets at station 107 and the season of greatest abundance of the other species is January to March when anchovy are least abundant.

The midwater complement of species regularly caught at this station is smaller, principally Pacific herring from January to June with jacksmelt characterizing the catch from April to December.

In the otter trawl shiner perch and bay goby are predictable elements of the catch for three seasons from January to September. White croaker are very consistently present from April to December, and only slightly less so in the remaining months. Plainfin midshipmen, as at station 101, are regularly present in the summer.

In the otter trawl the same pattern is found as at station 101, of greater species diversity from January to March and higher predictability from January to June. On the other hand the species richness in the midwater trawl stays low throughout the year.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						18	177 218
Apr-Jun	NAC	PH	JACK	SP			14	1921 19999
Jul-Sep	NAC	JACK	PH				11	365 4271
Oct-Dec	NAC						18	221 1462

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	NAC	DAB				25	663 807
Apr-Jun	NAC	SP	BAY	DAB			23	472 967
Jul-Sep							16	207 813
Oct-Dec	NAC						17	119 172

Although located in the same segment as station 107, station 108 displays a very different pattern of species occurrence. Northern anchovy are not predictably present in all seasons, in fact the July to September catch of the otter trawl contains no species more than eight times. The most regularly caught species in the otter trawl at that season is the plainfin midshipman.

In the midwater trawl, northern anchovy regularly dominate the catch from April to December but in the period from January to March only jacksmelt were caught at least a third of the time. Pacific herring are found with greater regularity from April through September, in contrast to their earlier regular occurrence in the more southern stations.

Compared to the other stations in this channel, the otter trawl at station 108 is remarkably bare of regularly occurring species. Fish catch is similar to other stations and winter and spring show an increased number of species, but there are few that occur regularly. The commonly caught species are the two most frequently caught fish in South Bay, northern anchovy and shiner perch.

Segment SB10
Bay Study Station 109

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	PH	LFS				12	207 605
Apr-Jun	NAC	PH	SP	JACK			17	2118 17996
Jul-Sep	NAC	PH					14	2166 18745
Oct-Dec	NAC	PH					14	1631 5772

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	BROK	NAC	WCRK	BRN SMO	LEOP	30	1096 1173
Apr-Jun	WCRK	BROK	BAY	MID	BRN SMO	NAC	27	505 580
Jul-Sep	NAC	BROK	SP	BAY	WCRK	MID	23	601 661
Oct-Dec	BROK	NAC	MID	WCRK			23	467 492

Station 109, in segment SB10, continues the trend of decreasing predictability of the fish fauna as one moves north from station 101. Northern anchovy and Pacific herring are the most abundant and consistent members of the midwater community and even in Oct-Mar, when at low catches, anchovy accounts for 66% and 85% of the midwater catch for the two quarters.

The otter trawl catch is strikingly different than the midwater catch. Species richness is high and many of the species are quite predictable. In addition northern anchovy makes up a very small part of the catch. This difference between the yield from each net probably reflects the greater depth of station 109 than any other channel station in South Bay, and so less overlap in the proportion of the water column sampled by the two nets.

White croaker and brown rockfish, are regularly caught at these stations in all seasons of the year. The occurrence of brown smoothhounds and plainfin midshipmen is earlier than at more southern stations, indicating the movement of these species from the ocean and down the channel. Underlining the greater proximity of this station to the ocean is the regular occurrence of leopard sharks.

B - 6

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	NAC	WCRK	LFS			14	946 1719
Apr-Jun	PH	NAC	WCRK	SP			23	3983 31890
Jul-Sep	NAC	PH	JACK	SP			17	2247 21278
Oct-Dec	NAC	PH					15	374 18911

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	WCRK	NAC	STAG	ENGL	LFS	26	967 1059
Apr-Jun	WCRK	NAC	BAY	MID	ENGL	BRN SMO	26	596 689
Jul-Sep	WCRK	BAY	SP	MID	ENGL	STAG	26	1861 1920
Oct-Dec	WCRK	SP	BAY	NAC	LFS		19	1087 1177

Tremendous abundance of northern anchovy in the midwater trawl is the dominant feature at station 110. Like the other station in SB10, station 110 generally yields most often Pacific herring and northern anchovy, but white croaker are also regular features of the catch from January to June and shiner perch often occur from April to September. Like the other station in this segment, species abundance peaks from April to June with low numbers of species from January to March when more southerly stations show their greatest species diversity.

The otter trawl catches a high diversity of species for most of the year and, many of them are quite regular and seasonal in their presence. White croaker and shiner perch dominate the catch year-round . (shiner perch are not included in the six most frequent species during spring in the table above but they were caught in more than a third of the trawls performed). They are joined regularly by English sole from January to March and by bay goby from April to December. As with station 109, plainfin midshipmen and brown smoothhounds occur earlier here than they do at stations further south.

East side stations
Segment SB5
Bay Study Station 102

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						8	114 312
Apr-Jun	JACK	NAC	PH	SP			14	495 2659
Jul-Sep	NAC	JACK					10	413 11844
Oct-Dec	NAC	JACK	TOP				8	639 1960

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL					26	375 426
Apr-Jun	SP	NAC	ENGL	BAY	STAG	WCRK	27	1562 1823
Jul-Sep	NAC	SP					27	278 965
Oct-Dec	NAC	SP					15	172 412

Station 102 in segment SB5 is the southernmost shallow station in South Bay. Northern anchovy is a regular feature of the catch from both nets, but is much more dominant numerically in the midwater net. In the midwater net jacksmelt are a regular feature with anchovy from April to December, while in the otter trawl, during the same months, shiner perch are captured with anchovies.

Species richness is low in the midwater trawl but high in the otter trawl for all of the year except from October to December.

Species predictability in the otter trawl catch is low for most seasons except spring, when 8 of the 27 species collected occur there in more than one third of the trawls made. The cheekspot goby is among those fish characterizing this station.

Segment SB8
Bay Study Station 104

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						8	94 211
Apr-Jun	NAC	JACK	SP	PH	WALL		22	549 1851
Jul-Sep	NAC	JACK	TOP				11	1974 12113
Oct-Dec	NAC						10	146 537

Otter trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL					25	325 442
Apr-Jun	NAC	SP	ENGL	BAY	STAG	PH	30	1116 1448
Jul-Sep	NAC	SP					24	349 918
Oct-Dec	NAC						14	142 459

Northern anchovy and jacksmelt are the most frequently caught fish in the midwater trawl and northern anchovy also dominate the otter trawl catch.

The midwater catch is characterized by the absence of any regularly caught species except anchovy from October to March. The walleye surfperch, which is not caught regularly at any other station on the eastern shore, is a regular inhabitant of this station during the period from April to June.

The otter trawl, as with station 102, dose not yield a very consistent catch except during the spring.

Bay Study Station 105

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						17	115 228
Apr-Jun	NAC	JACK	PH				13	1473 2598
Jul-Sep	NAC	JACK	PH				13	386 6764
Oct-Dec	NAC	JACK					10	502 1297

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL	DAB					29	260 298
Apr-Jun	SP	NAC	ENGL	DAB	STAG		29	968 1616
Jul-Sep	SP	NAC					21	417 703
Oct-Dec							18	73 504

The second station in segment SB8 is similar to the first; most of the predictability of catch is based on the more ubiquitous species of the South Bay. The midwater trawl results show that northern anchovy, Pacific herring and shiner perch are the only consistent catches throughout the year with the midwater trawl. Again, the otter trawl shows one period of lower species richness in October-December, and one period of high predictability in the spring.

West side stations
Segment SB 6
Station 103

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						9	117 197
Apr-Jun	NAC	JACK	PH	SP			15	1308 12953
Jul-Sep	NAC	JACK	TOP				9	289 12124
Oct-Dec	NAC	TOP	JACK				13	263 850

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL						29	307 328
Apr-Jun	SP	ENGL	STAG	BAY	NAC	DAB	26	1976 2654
Jul-Sep	SP	NAC					23	565 1427
Oct-Dec	SP						26	254 491

The wide shoals on the west side of South Bay are sampled at two stations. Station 103 is at the south end of the shoals. The regular midwater catch includes northern anchovy in all seasons except from January to March, but is remarkable for the year-round presence of jacksmelt. The most consistent catch in the otter trawl is shiner perch except for January to February when English sole is the only one of 29 species to be collected more than eight times in the 27 trawls performed.

As on the east side, only the spring months from April to June display much consistency of catch.

Station 106

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar							14	93 119
Apr-Jun	PH	NAC	JACK	WALL			21	6593 12197
Jul-Sep	NAC	SP	JACK	WALL	PH		16	1467 11143
Oct-Dec	NAC	JACK					12	609 2917

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL					26	349 387
Apr-Jun	BAY	SP	ENGL	WALL	NAC	WCRK	26	2918 2990
Jul-Sep	SP	BAY	NAC	ENGL	DAB	WALL	27	1673 2431
Oct-Dec	NAC						24	334 1328

Station 106 is located at the north end of the westside shoals. As with station 103 to the south, the midwater catch most often consists of northern anchovy and jacksmelt, but here both species are regular only during the period from April to December. From January to March there is no consistently caught species. Commonly occurring here, but not regularly at most other sites, is the walleye surfperch during the months from April to September.

In the otter trawl there is an assemblage of fish similar to that characterizing station 103 but here the group (containing shiner perch, walleye surfperch, English sole and bay goby) persists as a regular feature of the catch into the summer months.

Central Bay
Segment CB3
Station 213

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						11	115 1017
Apr-Jun	PH	NAC	KS				18	2213 29348
Jul-Sep	PH	NAC	JACK				13	4956 27295
Oct-Dec	PH	NAC					12	270 2802

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DAB	NAC	LFS				27	200 238
Apr-Jun	WCRK	NAC	LFS	ENGL	MID	DAB	26	345 610
Jul-Sep	MID	DAB	WCRK	LFS	NAC	SP	32	772 827
Oct-Dec	MID	LFS	NAC				22	462 535

Segment CB3 includes the Golden Gate and the deepest station sampled by the Bay Study is station 213 (24 m). Midwater trawl catch is largely northern anchovy which are common at most stations. Of particular interest is the regular catch of outmigrating chinook salmon smolts during the season from April to June and their absence in the catch from January through March. Species richness in the midwater trawl peaks at this time.

The greater sampling depth of the otter trawl is reflected in the much smaller catch of anchovy, which is not as regularly caught as other species in all seasons. The more regular occurrence of longfin smelt in the otter trawl than in the midwater trawl seems noteworthy. Plainfin midshipmen are most often caught from April to December while speckled sanddabs are caught most regularly from January to September. White croaker, English sole and shiner perch contribute to greater predictability of the otter trawl catch in the months from April to September. Species richness in the otter remains high through the year.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	PH	LFS	JACK				19	621 2109
Apr-Jun	PH	NAC	JACK	WCRK	KS		20	3655 17370
Jul-Sep	NAC	PH	JACK				19	3362 33005
Oct-Dec	NAC	PH					13	187 10731

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL	WCRK	DAB	STAG	LFS	31	2270 2368
Apr-Jun	ENGL	STAG	DAB	WCRK	NAC	SP	29	2186 3742
Jul-Sep	WCRK	BAY	STAG	NAC	ENGL	SP	29	5296 5480
Oct-Dec	WCRK	SP	NAC	ENGL	LFS	DAB	25	2994 3106

The deep channel running north-south between Alcatraz and the Berkeley mudflats is the second deepest station in Central Bay (16 m). The midwater catch shows the same domination by herring and anchovy as at station 213 on the west side of Alcatraz, although northern anchovy are slightly less regular from January to March. Chinook salmon smolts regularly pass through between April and June and are absent from January to March. Jacksmelt are regular features of the catch for most of the year.

The otter trawl samples a high density, species rich and very predictable fish assemblage. Shiner perch, English sole and white croaker are regular inhabitants year round. Speckled sanddabs are common in the three seasons from October to June and staghorn sculpins are regularly caught in the three seasons from January to September. Longfin smelt occur in catches from October to March, and are regular in the midwater trawl in the period when anchovy are least common.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	NAC	JACK				15	302 398
Apr-Jun	NAC	PH	LFS				19	1400 16895
Jul-Sep	NAC	PH	LFS	JACK	SP		20	2155 42079
Oct-Dec	NAC	PH					15	159 17717

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	ENGL	STAG	LFS	WCRK	DAB	32	2811 2853
Apr-Jun	DAB	WCRK	ENGL	NAC	LFS	BAY	29	1863 1930
Jul-Sep	ENGL	STAG	LFS	WCRK	MID	SP	31	4368 4461
Oct-Dec	SP	WCRK	LFS	ENGL	MID	BROK	24	1445 1509

The second station in segment CB2 is closer to San Pablo Bay which is reflected in the increasing regularity of longfin smelt in the catch, even outnumbering northern anchovy during the seasonal low in anchovy abundance. Otherwise the midwater samples are quite similar to those of station 214. Chinook salmon were taken in seven of the 27 trawls performed from April to June but in none of the preceding season.

The otter trawl fish catch is also very similar at the two stations, however longfin smelt are caught year-round with English sole and white croaker. Shiner perch is a slightly less regular feature of the catch. Plainfin midshipmen enter the catch from July through December, whereas speckled sanddabs are regular only from January through June. At both stations number of species is high year-round, particularly in January-March, and numbers of fish is high year-round with a peak from July through September.

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	PH	NAC				17	736 1372
Apr-Jun	NAC	PH	LFS	WCRK	KS	JACK	23	4825 19327
Jul-Sep	NAC	PH	SP	LFS	JACK	WCRK	20	2420 36225
Oct-Dec	NAC	PH					17	677 16756

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	STAG	SP	NAC	DAB	ENGL	26	632 673
Apr-Jun	LFS	ENGL	WCRK	DAB	NAC	STAG	27	1327 1416
Jul-Sep	STAG	LFS	NAC	DAB	SP	MID	26	651 747
Oct-Dec	LFS	NAC	ENGL	SP			24	1318 1736

Station 216 is in segment CB11, the northern channel of Central Bay leading into San Pablo Bay. The catch is very similar to that of station 215 but the increasing shallowness contributes to greater similarity between the midwater and otter trawls. The regular catch of white croaker from April to June is probably due to this shallower depth. Chinook salmon again enter the catch regularly in the months from April to June but are absent January to March.

The otter trawl catch is somewhat less abundant and diverse than in the southern stations. Aside from anchovies, only longfin smelt and English sole are commonly caught year-round. Shiner perch are again less dependably present in the spring.

Segment CB7
Station 211

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						23	398 420
Apr-Jun	PH	NAC	SP	KS	WCRK		22	2976 33836
Jul-Sep	NAC	PH					21	4625 55567
Oct-Dec	NAC	PH	JACK	WCRK			21	349 8927

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SP	DAB	ENGL	LFS	NAC	WCRK	28	2572 2808
Apr-Jun	WCRK	ENGL	DAB	SP	LFS	NAC	28	2183 2256
Jul-Sep	WCRK	NAC	SP	LFS	ENGL	DAB	26	3152 3326
Oct-Dec	NAC	ENGL	SP	STAG			20	1024 2497

Segment CB7 contains the shallower areas near the Berkeley waterfront. Northern anchovy and, to a lesser extent, Pacific herring are the most abundant and regular feature of the trawl. Chinook salmon are present regularly from April to June and absent in earlier months.

In the otter trawl the same six species make up the regular catch from January to September: northern anchovy, shiner perch, English sole, longfin smelt, speckled sanddab, and white croaker. Species richness and abundance are also high through these months. During October to December the total catch and the number of species declines and sanddabs, croaker and smelt are unpredictable. At this time, though, staghorn sculpins are regularly captured.

Station 212

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	JACK						14	79 124
Apr-Jun	NAC	PH	SP	JACK	WALL		17	1593 31000
Jul-Sep	NAC	JACK	SP	WALL	PH		16	1063 6605
Oct-Dec	NAC	JACK					16	948 1968

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC	ENGL	SP	DAB	SF		33	663 785
Apr-Jun	SP	BAY	ENGL	NAC	WCRK	SF	25	1745 4236
Jul-Sep	SP	ENGL	NAC	SF	BAY	STAG	24	1557 1918
Oct-Dec	NAC	SP	SF				16	292 1233

Station 212, in segment CB7, is the only shallow (3 m) station in the Central Bay. Jacksmelt is the only species regularly found year-round in the midwater trawl. Shiner perch and walleye surfperch are regular features of the catch from April to September. Species richness is low year-round and abundance sharply declines from January to March. Chinook salmon are seldom collected at this site.

The otter trawl shows a different species assemblage at this site; starry flounder, which are not regularly captured elsewhere in Central Bay, occur regularly year-round at this site with shiner perch and northern anchovy. English sole are less regular from October to December than the rest of the year. Other species are regular for shorter periods of the year than in the nearby channel stations.

San Pablo Bay Channel Station
Segment SP4
Station 325

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	NAC				22	1302 1868
Apr-Jun	NAC	LFS	PH	JACK	KS	WCRK	22	4071 16414
Jul-Sep	NAC	PH	MID	LFS	JACK		15	1449 36882
Oct-Dec	NAC	LFS	SB	PH			18	562 2013

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	YFG	STAG	SB	SP	ENGL	28	1225 1260
Apr-Jun	LFS	NAC	WCRK	STAG	MID	BAY	23	2115 2289
Jul-Sep	LFS	MID	WCRK	NAC	STAG	BAY	23	1749 1834
Oct-Dec	LFS	STAG	MID	WCRK			22	1559 1621

As with Central Bay, the deep station in San Pablo Bay is dominated by the regular appearance of northern anchovies in the midwater trawl in all seasons of the year, with Pacific herring commonly occurring in the catch from April to December. Unlike any of the stations further downstream, though, striped bass are a regular feature of the fish assemblage from October to March. Jacksmelt commonly occur in the months from April to September. Chinook salmon regularly occur in the trawls from April to June.

The fish assemblage from the otter trawl is quite different than at sites downstream; staghorn sculpin is a regular part of the catch year round and longfin smelt is the most frequently encountered species in all seasons of the year. Plainfin midshipmen and white croaker enter the catch for most of the year (April to December) and bay gobies, like jacksmelt in the midwater trawl, are regular parts of the seasons collections.

North side stations
Segment SP3
Station 323

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	NAC						12	117 124
Apr-Jun	NAC	PH	JACK	LFS	SP		17	3225 14589
Jul-Sep	NAC	PH	JACK				17	459 15946
Oct-Dec	NAC						15	281 6118

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	YFG	SF	SB	STAG		23	579 590
Apr-Jun	STAG	BAY	NAC	WCRK	LFS	ENGL	23	1892 2422
Jul-Sep	STAG	NAC	BAY	MID	WCRK	SP	21	2763 3016
Oct-Dec	NAC	LFS					22	1014 1183

Northern anchovy is the only regular feature of the midwater trawl catch for all seasons. During the season from April to September Pacific herring and jacksmelt also occur regularly. Generally the catch is depauperate and small except for the large seasonal influx of anchovy.

The otter trawl catch is dominated by the regular catch of longfin smelt and staghorn sculpin for three seasons of the year. Bay goby and white croaker are a regular part of the April-September catch. This is the furthest downstream station where striped bass and yellowfin goby are regularly captured.

Station 322

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						9	194 266
Apr-Jun	NAC	JACK	PH	LFS			15	3052 6470
Jul-Sep	NAC	SP	JACK				17	2209 16405
Oct-Dec	NAC	AMS					11	163 2210

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	STAG				20	704 717
Apr-Jun	BAY	ENGL	STAG	SF	WCRK	NAC	20	2607 2910
Jul-Sep	NAC	SP	STAG	YFG	SF	SB	20	1363 1788
Oct-Dec	NAC	LFS	SF				14	395 846

The midwater trawls at this station, in the middle of the shallow area of San Pablo Bay, is characterized by the increased dominance by longfin smelt and by the seasonal presence of American shad. Jacksmelt and shiner perch are regular features in spring and summer.

The otter trawl catch shows greatest predictability from April to September when several species that are more common in South and Central Bays appear to invade San Pablo Bay, including bay goby, English sole, and white croaker. Starry flounder are the most frequently captured flatfish. Striped bass are more regular here than at station 323 downstream.

Station 321

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						15	218 225
Apr-Jun	NAC	PH	JACK	LFS	SP		15	2350 12177
Jul-Sep	NAC	LFS	JACK	SB	SP		19	1899 21842
Oct-Dec	NAC	LFS	AMS				12	279 2943

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	492 505
Apr-Jun	STAG	LFS	ENGL	NAC	SF	WCRK	20	1941 2272
Jul-Sep	NAC	SF	STAG	YFG	SP	LFS	17	2745 3148
Oct-Dec	NAC	LFS	SB	SF			15	636 1056

Longfin smelt dominate the catch in all seasons in both nets at station 321and is the only regular feature of the midwater catch from January to March. In the midwater trawl, American shad are a regular feature, as they were at station 322. This is the furthest downstream site where striped bass are a regular feature in the midwater trawl. Jacksmelt and shiner perch regularly enter the catch in the months from April to September.

In the otter trawl, starry flounder are regularly abundant from April to December. Warmer months are accompanied by regular occurrences of several species, while the wetter months support fewer regular species. Striped bass occurs regularly from October through March but is irregularly caught in warmer months.

Segment SP2
Station 320

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	SF				14	566 570
Apr-Jun	NAC	LFS	JACK	PH	SB		20	4478 14104
Jul-Sep	NAC	LFS	JACK				14	1531 18965
Oct-Dec	NAC	AMS	SB	LFS			17	514 2915

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SF	SB	STAG			17	565 579
Apr-Jun	LFS	STAG	NAC	SF	ENGL	SB	25	2407 2738
Jul-Sep	NAC	SB	SF	STAG	LFS	SP	18	1421 2692
Oct-Dec	SB						12	347 553

The midwater trawl at the northernmost station in San Pablo Bay reflects the trend in species composition that is displayed in the series of downstream stations. Longfin smelt are regularly caught in all seasons, striped bass are found through most of the year, jacksmelt are present during from April through September and Pacific herring are regular only in spring. The increasing dominance of the otter trawl catch by starry flounder is reflected in the regular catch of starry flounder in the midwater trawl and is explained by the fact that this is the shallowest station in San Pablo Bay (2.6 m).

The otter trawl is regularly characterized by the presence of four species that are less common in the downstream embayments: longfin smelt, striped bass, starry flounder and staghorn sculpin. Species richness is low, but rises in the summer with the regular appearance of species more common downstream: shiner perch, northern anchovy and English sole.

East side stations
Segment SP5
Station 317

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar							21	1336 1343
Apr-Jun	PH	NAC	JACK	SP			24	1474 8694
Jul-Sep	NAC	JACK	PH	SP	WALL		20	1074 20180
Oct-Dec	NAC	JACK					10	188 1292

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	ENGL	LFS	SB	STAG	SP	BAY	30	890 897
Apr-Jun	ENGL	STAG	SF	SP	BAY	LFS	33	1606 1676
Jul-Sep	NAC	SP	ENGL	BAY	STAG	SF	23	2716 3468
Oct-Dec	NAC						18	243 450

The midwater catch at station 317 records 21 species and 1343 individuals, but none occurred in more than 8 of the 27 trawls during January to March. The remainder of the year was consistently made up of northern anchovy and jacksmelt, with shiner perch and Pacific herring from April to September. This is the most upstream site where walleye surfperch are regularly caught.

Otter trawl catches show a consistent set of species through the first nine months of the year: English sole, Staghorn sculpin, shiner perch, bay goby. At the start of the water year all these species fall to much less predictable status, species richness drops to about half of that in the January-June, and fish abundance is very low. Striped bass regularly show up in the catch for January to March and longfin smelt arrive and consistently persist through June.

Segment SP6
Station 318

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						22	470 490
Apr-Jun	NAC	PH	JACK				21	3459 11981
Jul-Sep	NAC	JACK	SP	PH			19	974 14854
Oct-Dec	NAC	AMS	JACK				12	238 3742

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	YFG	ENGL	SF	LFS	BAY	25	639 665
Apr-Jun	STAG	BAY	ENGL	WCRK	SP	LFS	23	1537 1647
Jul-Sep	NAC	SP	SF	STAG	SB	LFS	22	2714 3330
Oct-Dec	NAC						16	361 599

As in the shallow stations on the north side of San Pablo Bay, American shad are a regular feature of the midwater catch at Station 318 from October to December. As at the shallow stations on the other side, jacksmelt and Pacific herring regularly enter the catch starting in the April but here jacksmelt stay into the October-December season.

The fishes of the otter trawl are regular in their occurrence at this station but there is less consistency across seasons, most are present consistently for only one or two species, only longfin smelt are regular across three seasons. As at the other stations, the start of the water year coincides with a sharp decline in number of species, number of fish and consistency of catch across years.

Station 319

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	286 382
Apr-Jun	NAC	PH	JACK				15	1126 10892
Jul-Sep	NAC	JACK	SB				13	677 18634
Oct-Dec	AMS	NAC					12	152 776

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS	YFG	ENGL	STAG	26	1484 1514
Apr-Jun	STAG	ENGL	NAC	SF	SP	LFS	21	3330 3472
Jul-Sep	SF	SB	NAC	SP	LFS	STAG	21	3681 3904
Oct-Dec	SB						12	328 345

The third station on the shallows of the east side of San Pablo Bay (319) is very similar to station 320 at the uppermost range of shallows on the other side of the channel.

Like 320, 319 regularly catches American shad and striped bass in the midwater trawl, with jacksmelt entering the catch from April to September, and with Pacific herring regularly occurring in only one season. Unlike 320, the midwater trawl only regularly catches longfin smelt from January through March, instead of year-round

The otter trawl catch is very similar on the two sides of the channel. The same set of four species is present in three seasons: longfin smelt, starry flounder, striped bass, and staghorn sculpin. Northern anchovy and shiner perch again enter the catch primarily during the months from April to September. Finally, the number of species, number of fish, and number of consistently captured species all fall drastically in the season from October to December, leaving striped bass as the only dependable part of the catch.

Carquinez Straits
Segment SP7
Station 427

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	1346 1371
Apr-Jun	LFS	NAC	SB				18	1009 3397
Jul-Sep	NAC	SB	LFS	MID	PH		16	753 20361
Oct-Dec	LFS	SB	NAC				15	2612 3628

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	STAG				19	367 374
Apr-Jun	LFS	NAC	STAG				17	340 395
Jul-Sep	LFS	NAC	SB	STAG	MID	YFG	14	611 733
Oct-Dec	SB	LFS	STAG				11	465 478

This station falls within the San Pablo embayment scheme of Gunther (1987) as segment SP7 but the fish fauna is obviously much more like that of Suisun Bay. Longfin smelt and striped bass are regularly found in the trawls of both nets in all seasons (except for the low predictability in catch of striped bass in the otter trawl for the April-June season). Plainfin midshipmen occur in both trawls in the summer months. Northern anchovy are rarely caught in the months from January to March, but are common in other seasons. Staghorn sculpin is the only bottom species caught consistently year-round. None of the flatfish are regularly captured here in any season and yellowfin goby are found in the otter trawl during the months from July to September.

Suisun Bay Channel stations
Segment SU1
Station 428

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					13	1564 1564
Apr-Jun	LFS	NAC	PH	SB			16	1240 3091
Jul-Sep	NAC	SB	LFS				13	1515 4463
Oct-Dec	LFS	SB	NAC	AMS			12	858 2800

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	YFG				16	390 391
Apr-Jun	LFS	STAG	NAC				16	1394 1448
Jul-Sep	STAG	NAC	YFG	LFS	SB		12	801 842
Oct-Dec							13	212 227

Midwater trawls at station 428 consistent include longfin smelt and striped bass in al seasons of the year. Northern anchovy invade from April to September and young American shad pass through from October through December.

Otter trawl catches are much less consistent and in winter there is no species found in more than one third of the trawls performed. In the first nine months of the year longfin smelt are the most regular part of the catch. Species richness is much lower than in downstream and number of individuals is about half of that found at the channel station in San Pablo Bay. Northern anchovy seasonally enters the catch, but at very low numbers.

Station 432

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	830 831
Apr-Jun	LFS	SB	PH	NAC			15	895 2788
Jul-Sep	NAC	SB	LFS				14	408 1338
Oct-Dec	SB	LFS	AMS				15	1244 1292

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LFS	STAG	YFG			13	325 325
Apr-Jun	STAG	LFS	YFG	SF	SB		17	657 666
Jul-Sep	SB	STAG	SF	YFG	LFS		17	672 689
Oct-Dec	STAG	SB	LFS				11	290 292

Station 432 is close to station 428 and the midwater trawl catches are almost identical, although fish abundance is lower and fewer anchovy are found here.

The otter trawl catch, however, is much more predictable than at station 428. This reflects the fact that this station is at the edge of the shallow stations of Suisun Bay where the fish community is very similar and predictable. Striped bass, longfin smelt, and staghorn sculpin are regularly caught year round and yellowfin goby are regular residents of three seasons. Starry flounder are regular members of the benthic community during summer months.

Station 429

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					16	766 768
Apr-Jun	LFS	NAC	SB				13	958 1721
Jul-Sep	SB	NAC	LFS	YFG	DS	AMS	14	2251 4067
Oct-Dec	LFS	SB	NAC				14	1513 2061

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					15	263 263
Apr-Jun	LFS	YFG	SB	STAG			17	866 885
Jul-Sep	SB	STAG	YFG	LFS	NAC	SF	13	795 856
Oct-Dec	LFS						11	565 566

Midwater catch at station 429, at the mouth of Grizzly Bay, usually contain longfin smelt and striped bass in each season. American shad regularly occur at this site between July and September, earlier than they do at downstream sites. This is the most downstream station at which delta smelt occur regularly, in summer.

Otter trawl catches also regularly contain longfin smelt throughout the year; striped bass are found regularly in all seasons except October to December. During summer months starry flounder, yellowfin goby and staghorn sculpin are a regular part of the catch.

Station 433

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					11	329 329
Apr-Jun	LFS	KS	SB	NAC			10	432 712
Jul-Sep	SB	LFS	AMS	NAC	YFG		15	1358 1936
Oct-Dec	SB	LFS	AMS				15	2118 2328

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					12	145 145
Apr-Jun	LFS						15	522 531
Jul-Sep	SB	YFG	LFS	SF			12	455 485
Oct-Dec	LFS						9	499 500

Like the other, downstream, shoal stations of Suisun Bay the midwater catch at station 433 is dominated by longfin smelt and striped bass in all seasons of the year. Northern anchovy invade during the summer. American shad are regularly caught in the period from July to December.

The otter trawl catch is small throughout the year. Longfin smelt are commonly caught in all seasons. Other species common in Suisun Bay are sometimes listed as regularly occurring, but the lack of consistent catch is probably a reflection of small total catches.

Segment SU2   Suisun and Grizzly Bay shoals
Station 430

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB	DS				10	162 162
Apr-Jun	SB	PH	LFS	NAC			16	669 1051
Jul-Sep	SB	NAC	LFS	ST	AMS	YFG	18	3517 4264
Oct-Dec	LFS	AMS					14	1242 1727

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS	YFG			15	430 430
Apr-Jun	SB	YFG	LFS	STAG	SF		15	1192 1197
Jul-Sep	SB	YFG	STAG	SF	LFS	NAC	14	1789 1823
Oct-Dec	SB	LFS	YFG	STAG	SF		12	726 732

Station 430 is near the mouths of Suisun Slough out of Suisun Marsh and of Montezuma Slough which carries Sacramento River water. The station shows high consistency in the catch of both nets within a context of low species diversity. Like the midwater trawls of the channel stations, longfin smelt are present year round and striped bass are caught regularly in most of the year except October-December. American shad appear in the trawls from July to September. Delta smelt is regularly caught in January to March and splittail are regularly caught from July to September; these species appear to be characteristic of shallower habitats, with splittail maintaining a large part of its population in the shallow sloughs of Suisun Marsh.

The midwater trawl largely consists of repeated captures of a core of five species: striped bass, yellowfin goby, longfin smelt, starry flounder, and (in three seasons) staghorn sculpin. This consistency is particularly remarkable because these species comprise a third of the total number of species that have ever been caught here.

Station 431

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DS	LFS	SB				13	250 250
Apr-Jun	SB	NAC	PH	LFS			14	388 753
Jul-Sep	SB	NAC	LFS	AMS	DS	ST	13	973 1698
Oct-Dec	LFS	SB	AMS	DS	NAC		13	1392 1503

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF	LFS				16	408 408
Apr-Jun	SB	SF	LFS	YFG	STAG	ST	18	627 639
Jul-Sep	SB	SF	YFG	LFS	STAG	NAC	16	3491 3523
Oct-Dec	SB	LFS	YFG	STAG	SF		10	731 737

Station 431 is on the south side of Grizzly Bay, opposite station 430 . Midwater trawl catch is almost identical at the two stations except that delta smelt is caught July through January which doubtless reflects the fact that adult delta smelt have moved out to spawn and die and that the young are too small to be collected in the trawl. The regular occurrences of anchovy, American shad and splittail are identical to those at station 430.

Otter trawl catches are also very similar at the two stations, with a set of five species dominating all aspects of the catch. Striped bass, starry flounder, longfin smelt are found in all four seasons while yellowfin goby and staghorn sculpin are regularly present from April through December. The absence of delta smelt from the otter trawl while they are present in the midwater trawl at this shallow station (3 m) emphasizes the presumed surface orientation of this fish.

Segment SU 3 Honker Bay shoals
Station 534

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	DS					13	184 184
Apr-Jun							13	133 248
Jul-Sep	SB	NAC	AMS	LFS	WS	DS	16	2931 3083
Oct-Dec	LFS	SB	AMS	DS			12	690 913

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	SF					12	224 224
Apr-Jun	SB	SF	YFG				14	723 724
Jul-Sep	SB	YFG	LFS	SF	ST		16	4126 4130
Oct-Dec	SB	LFS					14	915 915

Station 534 in Honker Bay is very different than the similar shoal stations in Grizzly Bay. The midwater trawl shows extremely low catches from April to June, with no species being caught consistently. Longfin smelt and delta smelt are the most regular part of the catch. As at other stations in Suisun Bay, American shad are present regularly from July through December. Uniquely, white sturgeon are caught regularly at this station; these are not young of year as is the case for several other seasonal catches (sizes range from 304 to 671 mm SL).

Otter trawl catch is dominated by striped bass in all seasons and starry flounder for all periods except October-December. Longfin smelt are regular only in summer months. The seasonal catch of splittail is one point of similarity with the catch in Grizzly Bay.

Western Delta
below confluence of Sacramento and San Joaquin
Station 535

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					11	248 248
Apr-Jun	KS	LFS	SB				13	254 331
Jul-Sep	SB	LFS	AMS	DS	YFG	NAC	15	2931 3083
Oct-Dec	LFS	SB	AMS				12	613 670

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS						14	147 147
Apr-Jun	LFS						17	367 369
Jul-Sep	SB	LFS	YFG				12	847 851
Oct-Dec	LFS	SB					15	366 382

Catch at this station is very similar to the channel stations downstream in Suisun Bay. Longfin smelt and striped bass are found year-round. American shad enter and pass through from July to December, chinook salmon smolts pass through from April to June and northern anchovies enter in the summer. Delta smelt are a regular member of the midwater catch in July through September as they are downstream at station 429.

Like the other deep channel stations above Carquinez Straits, the otter trawl catch is not very predictable; longfin smelt occur year round and striped bass are regularly caught from July through December.

Sacramento River channel
Station 736

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					14	202 202
Apr-Jun	KS	SB					12	179 180
Jul-Sep	SB	AMS	DS				13	1734 1759
Oct-Dec	LFS	SB	DS				11	386 397

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	LFS	SB					12	94 94
Apr-Jun	WCAT						15	279 279
Jul-Sep	SB	WCAT	YFG				13	656 656
Oct-Dec	SB	LFS					13	287 287

Midwater catches at the lower Sacramento River site show the effect of location on seasonality of catch in three migratory species. Chinook salmon and American shad are collected here only in the season prior to their capture at downstream sites. Delta smelt are caught from July on December, probably reflecting their upstream spawning migration from the downstream sites where they are generally collected in the first three seasons of the year. Longfin smelt are collected in both nets only from October to March, which encompasses their likely time of upstream migration from their usual habitat in Suisun and San Pablo Bays. Only striped bass are regularly caught at this site year-round.

The otter trawl catch is very depauperate and catches are very small but this station is unique in that white catfish is a regular element from April through September.

San Joaquin River (shallow channel station)
Station 837

Midwater Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	DS						6	111 111
Apr-Jun	KS						8	106 106
Jul-Sep	AMS	SB					8	1237 1237
Oct-Dec	AMS	SB	TFS				9	346 346

Otter Trawl
Species Rank

	1	2	3	4	5	6	spp.	catch
Jan-Mar	SB	LOGP					13	261 261
Apr-Jun	SB	SF					13	350 350
Jul-Sep	SB						12	670 670
Oct-Dec	SB						12	363 363

In the San Joaquin River catches in both nets are very low and few species are consistent in their occurrence (which may just reflect the extremely low numbers).

The midwater net displays lower species richness than at any other station in the estuary. This station is also unique in that no anchovies have ever been captured here. Longfin smelt are also a very rare species at this station, making it different than any other station above Point Richmond. The other migratory species found in the Sacramento River similarly pass through this site, but at lower densities. Unique to this site is the presence of threadfin shad at the start of the wet season. As discussed in the section on threadfin shad, this is not an actual migration, but rather a simple washout which carries the shad into cooler waters downstream, with a subsequent winter die-off.

The otter trawl catches striped bass year-round but is distinguished in January to March by the regular presence of bigscale logperch.